

PRODUCTIVITY OF FLORIDA SPRINGS

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Second Annual Report

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Progress from January 1 to December 31, 1954

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## INTRODUCTION

1

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PRINCIPLE INVESTIGATOR: (This project is administratively listed under W. C. Allee, Head of the Biology Department).

Howard T. Odum (February 1 - September 1, 1954)

James L. Yount (September 1, 1954 - January 31, 1955)

Associate: Delle Natelson (September 1, 1954 - June 15, 1955)

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F. H. Berry (June 1 - September 1, 1954)

D. K. Caldwell (September 1, 1954 - January 31, 1955)

TITLE OF PROJECT: PRODUCTIVITY OF FLORIDA SPRINGS

Objectives: A study of basic factors that control productivity and of the effects of productivity on community structure and density by an analysis of the unique conditions supplied by selected constant temperature springs.

### ABSTRACT:

#### a. During current report period

Production measurements at different times of the year indicate a linear relationship of light intensity and overall production at about 8% of the visible light energy reaching plant level. Measurements of a coral reef at Eniwetok indicate 6%. Further evidence of breeding at all seasons but with a quantitative pulse in the seasons of maximum light indicates that the seasonal fluctuation in primary production is routed through reproduction rather than through major changes in populations. The succession of plants and animals of the aufwuchs has been shown with glass slides and counts from Sagittaria blades. Loss of oxygen bubbles during the day and emergence of aquatic insects at night have been measured with funnels. Bell jar measurements are reported for bacterial metabolism on mud surfaces. pH determined CO<sub>2</sub> uptake agrees with titration determinations. A few rough estimates of herbivore production have been made from caged snails, aufwuchs succession, and fish tagging. Nitrate uptake at night by aufwuchs communities has been confirmed in a circulating microcosm experiment as well as in bell jars in the springs. Distributions of oxygen and organisms have been used to criticize the saprobe stream classification system. Theoretical consideration of maximum photosynthetic rates in literature data indicates logarithmic rate variation inversely with organismal size just as for respiratory metabolism. Extreme pyramid shapes are thus shown for communities in which organismal size decreases up the food chain and for other communities with the same energy influx but with organismal size increasing up the food chain. Literature data is used to further demonstrate the validity of the optimum efficiency--maximum power principle for Photosynthesis. Work on aquatic

## ABSTRACT (Cont'd.)

plants by Dr. Della Natelson indicates essential stability of aquatic plant communities after 3 years and about 10--20% reproducibility in previous biomass estimates by Davis. Work on an annual picture of the fishery characteristics by Caldwell, Berry, and Odum is half completed. The study of aquatic insects in relationship to spring gradients by W. C. Sloan has been completed as M. S. Thesis. J. Yount has begun a study of effect of total productivity on community composition using aufwuchs organisms on glass slides placed in different current and light conditions in Silver Springs.

## b. Since Start of Project

This contract was begun June 1, 1952. In the year and a half preceeding the present report period, work of a very varied nature outlined the trophic structure and metabolism of Silver Springs with comparisons made with other Florida springs. The intensive study of Silver Springs is now nearly complete and quantitative comparisons of productivity with other Springs will follow. Most of the techniques and approaches outlined in the original proposal have now been applied. The study of factors affecting qualitative community structure is the main incomplete phase.



## PLANS FOR FUTURE

## Immediate:

## 1. By J. L. Yount

Determine the relationship of productivity to the variety and the dominance of species comprising the various communities of a spring. This is to be done as follows:

a) by observation of the numbers of species per niche in single habitats within the spring, e.g., Aufwuchs on Sagittaria blades and glass slides in different regions of the spring where productivity differs but other factors are constant. Both high and low trophic levels will be studied.

b) determine relationships as above under experimental conditions in aquaria and other vessels. Plankton and Aufwuchs are expected to serve as the principal experimental groups, but other groups may also be examined.

## 2. By D. K. Caldwell, F. H. Berry, and H. T. Odum during Spring and Summer.

Complete an annual cycle of Fishery characteristics begun last spring as follows:

a) tag and recapture more fish

b) determine the significance of scale annuli in Silver Spring fish

c) further determine the extent of winter breeding of fishes in Silver's constant temperature waters

d) complete food assay of dominate fish species

e) determine growth rate of young stumpknockers in cages

f) determine the significance of length-frequency graphs of fish collected in springs throughout the year

## 3. By D. Natelson during Spring 1955

Compare the community composition of aquatic plants with communities not in constant temperature springs.

## 4. By H. T. Odum during summer 1955

a) Relate the overall community production of 20 springs measured by the downstream flow method to current velocity to test hypothesis that the overall primary productivity of communities in steady state is a function of velocity of water over plant surfaces.

b) Complete the picture of metabolism in Silver Springs by additional data on organic matter loss downstream, effects of side boils, herbivore growth, repetitions of quadrat measurements, spectrogram of water and plant ash.

## Long Range Plans

## 1. By J. L. Yount

a) determine relationship of productivity to variety and species dominance in other aquatic habitats, both inland and marine, contrasting habitats with high productivity and low productivity.

- b) define the relationship between productivity and competition.
2. By H. T. Odum (Duke University)
- a) apply method of measuring community structure and metabolism to other steady state systems such as Hot Springs and tropical streams.
  - b) construct microcosms in the laboratory to contain small steady state communities in order to further delimit principles.

#### REPORTS AND PUBLICATIONS

Supported in part by this project:

Odum, H. T. 1953. Dissolved phosphorus in Florida Waters. Report of Investigations #9, Fla. Geol. Survey, Tallahassee Fla. 40 pp.

In press:

Odum, H. T. and R. C. Pinkerton

Times Speed Regulator: The optimum efficiency for maximum power output in physical and biological systems.  
American Scientist

Odum H. T. and David K. Caldwell

Fish respiration in the natural oxygen gradient of an anaerobic spring in Florida.  
Copeia

Completed Thesis

Sloan, W. C. Some environmental factors influencing the distribution of aquatic insects in certain Florida Springs.

Manuscripts completed and submitted for publication:

Sloan, W. C. A comparative ecological study of the insects of two Florida Springs. (Submitted to Ecology).

Whitford, L. A. The Communities of Algae in the Springs and Spring Streams of Florida. (Submitted to Ecology).

Odum, H. T. and E. P. Odum. Trophic Structure and Productivity of a Windward Reef at Eniwetok, 90 pp. manuscript.

Manuscript in preparation

Odum, H. T. Trophic Structure and Productivity of Silver Springs Florida.

Howard T. Odum

Measurements and detailed studies continue on Silver Springs in an effort to determine the detailed workings of a fertile complex aquatic community in steady state.

#### A. Seasonal Trends in Production in Chemostatic Conditions

The upstream-downstream method of measuring productivity as reported in previous progress reports has now been carried out in Silver Springs in various seasons of the year and with different cloud covers. From these data an annual curve of total community primary production is drawn in Figure 1. The area under this curve is the total primary production. The horizontal line represents the respiration and downstream losses as previously determined. If the community is in steady state the area above the horizontal line should balance the area below. These areas do not quite correspond. Further refinements in measurement of downstream losses in the diffusion correction, and in the effects of side boils will be required to account for the fate of the excess production.

A curve for *Sagittaria* production from the planting experiments is also shown in Figure 1. The difference between this growth and the total production represents the algal production which turns out to be 70% of the total even though the *Sagittaria* biomass is greater. That most of the producing community is algae and *Sagittaria* is evident from plant maps of Silver Springs referred to in previous reports.

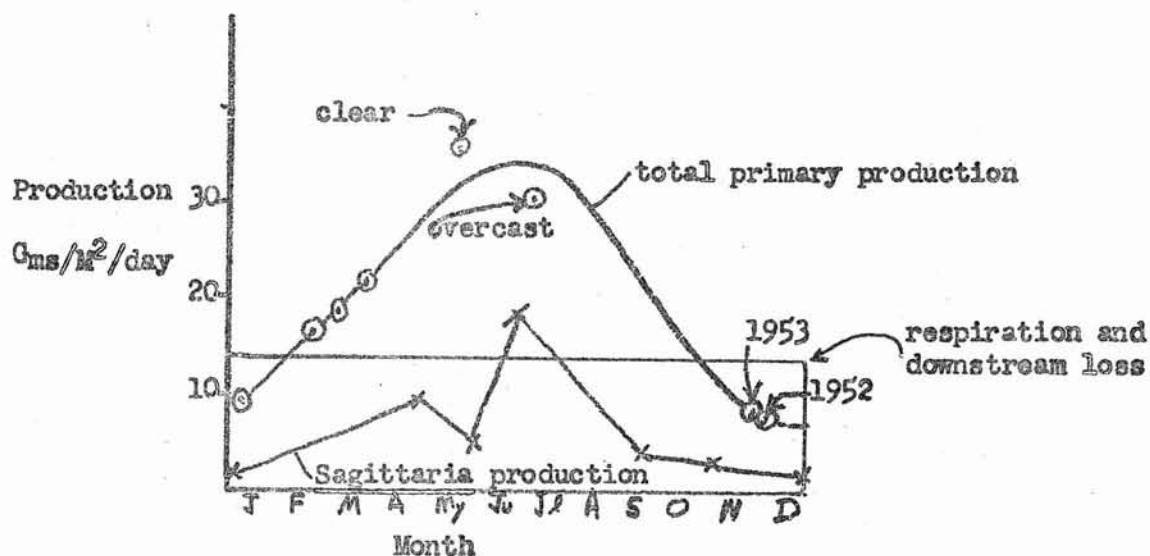


Figure 1. Annual Course of Primary Production

## B. Determination of the Light Intensity Reaching the Plants

In order to determine efficiencies of primary production, light intensities reaching the plants were determined as follows:

- (1) Insolation reaching the ground on a given date for a given cloud cover is determined from tables in Kennedy (1949. Bull. Amer. Meteor. Soc. 30:208-213.).
- (2) Half of this is taken as infra-red and half in the visible range
- (3) With a submarine photometer containing a weston photronic cell sensitive to visible wave lengths, the percent penetration to plant level at 8 ft is determined. A winter curve was shown on page 8 of the last progress report. A summer curve is now given in Figure 2 below.
- (4) The percent transmission for a given time of the year is interpolated between the two extreme curves represented by January and May. The difference between percent transmission is mainly due to a difference in angle of incidence.
- (5) The insolation reaching the spring community is diminished by shadows from trees especially when the sun is at a low angle. Due to the orientation of the spring and its tree pattern this effect is greatest in the morning as reflected in the asymmetry of the diurnal curves. The tree effect is greatest in the winter. There is little effect on cloudy overcast days when the light is diffuse.

To correct for the effect of trees, at least during the morning, the daily insolation curves mentioned above are redrawn so that the morning is symmetrical with the afternoon curve as shown in Figure 2. The area between the redrawn and original curve represents the light removed by the trees. No such correction is made for cloudy days. The correction on the winter curve is greater proportionately than on the summer curve.

Light intensities determined in this way are related to production below.

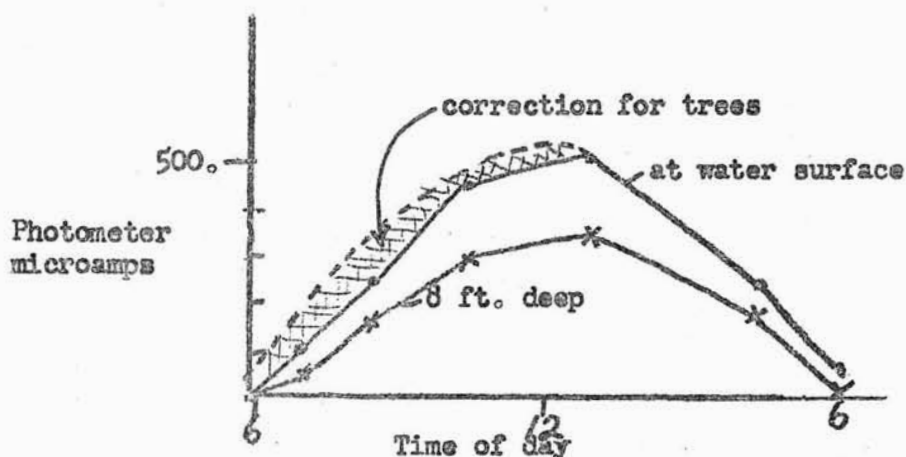


Figure 2. Diurnal March of Light, May 28, 1954

### C. Production as a Function of Light Intensity for the Whole Community

For each daily production figure given in Figure 1, a daily light intensity value was determined as described in paragraph B above. The graph in Figure 3 shows total community primary productivity as a function of light intensity of visible wave length reaching plant level. The horizontal line is the estimate of respiratory and downstream losses estimated from previous reports.

Apparently the production is proportional to the light intensity even at these relatively high light intensities. Most physiological experiments on single plants show decreasing efficiencies with increasing light intensity at high light intensities. It can also be noted that the community runs below its overall compensation point on cloudy winter days. This does not mean that individual plants do this for the community compensation point includes not only respiration but downstream losses. Possibly an explanation of the dumping of half the production downstream lies in a requirement that at steady state the single plants must nevertheless never be exposed to conditions below the individual compensation point. As seen below the coral reef does not do this and similarly does not have the low light of winter. Perhaps there is a generalization that temperate communities must produce excess organic matter as soil or peat or downstream loss which tropical communities need not do. From the data available it is not clear whether there is a break in the curve at the compensation point as discussed in the theoretical section. Actually the best fit to the points indicates an increasing efficiency with increasing light intensity. As discussed below this might be accounted for by increased respiration of plants which individually were below their compensation points on cloudy days in more shaded places.

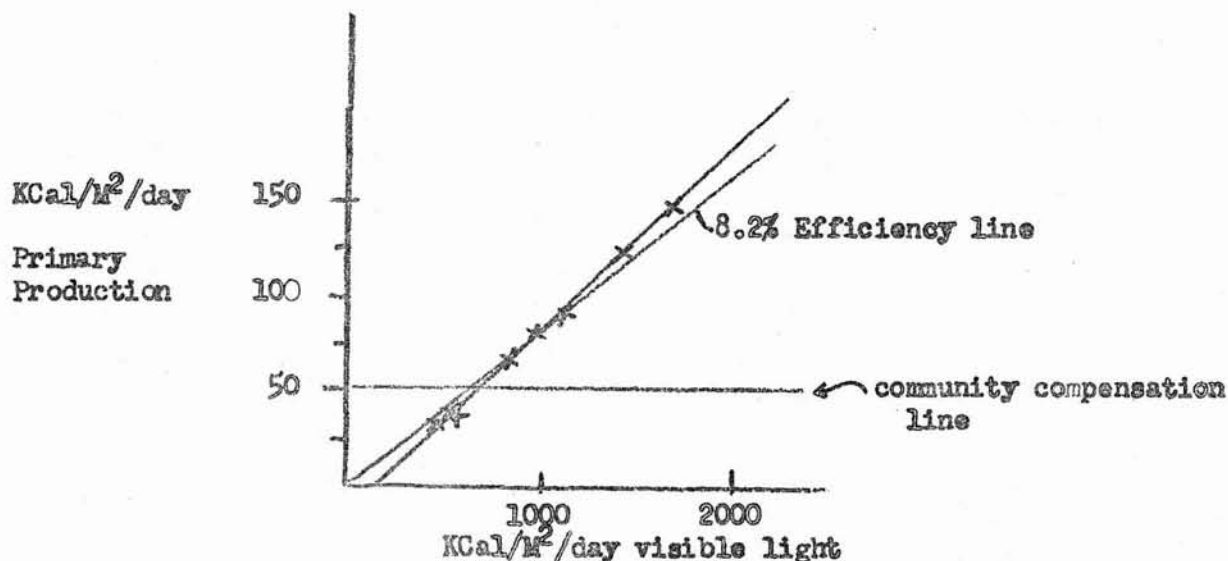


Figure 3. Community primary production v.s. light intensity



# D. Seasonal Pulse of Energy; Breeding and Photoperiodism

The graphs in Figures 1 and 3 indicate a strong pulse of energy in the spring and summer compared to the less lighted months. This is actually a greater difference in the aquatic community than on land because of the angle effect of the trees and water reflection.

One is accustomed to associating big seasonal differences in energy flux with succession and blooms among the planktonic organisms in lakes and in the ocean. It is interesting to consider the fate of the energetic pulse in Silver Springs where no large successional changes have been observed even in the microscopic algae of the aufwuchs.

In Figures 4 and 5 are shown annual pictures of breeding in the apple snail *Pomacea* which lays its eggs above the water line and in *Palaeomonetes* which carries its eggs. From these graphs it may be concluded that in these forms breeding occurs throughout the year in this constant temperature environment but at different rates that are likely to be photoperiodically controlled. Thus these species seem adapted to the energetic pulse of the whole community. As Forbes long ago described, the survival of any particular community complex requires the components to eat neither too much or too little. As mentioned in the report on Fishery studies below there is some evidence that similar round the year breeding occurs in the fishes with a large vernal pulse.

Fig. 4 Annual Reproduction of *Pomacea*

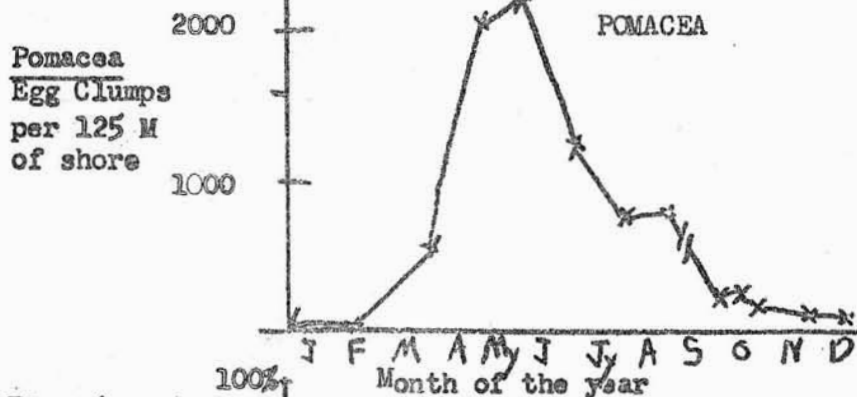
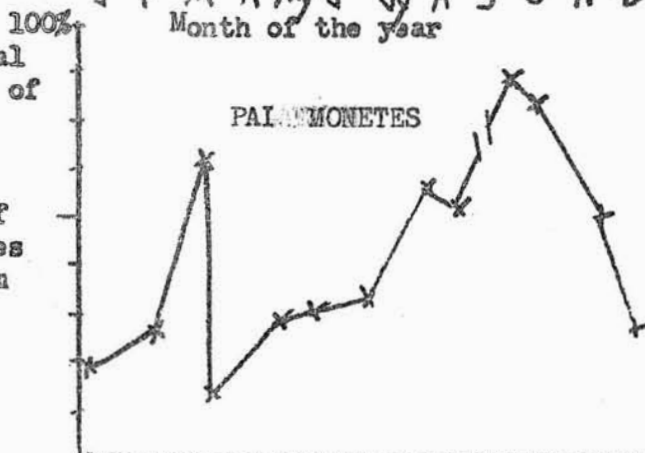


Fig. 5 Annual Reproduction of *Palaeomonetes*

Percent of the females over 21 mm with eggs



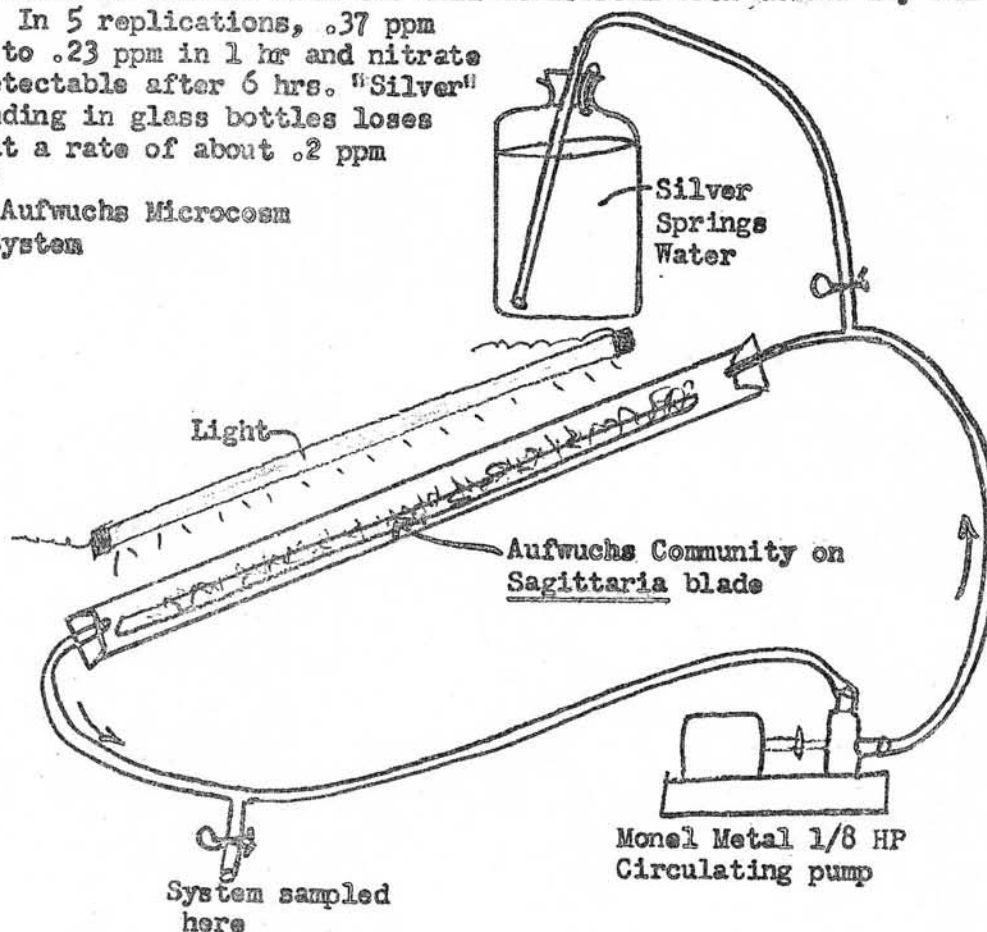
# E. Initial Aufwuchs Microcosm Experiment, Nitrate uptake in the Dark

As mentioned in the theoretical section below, microcosm experiments are a useful type of experiment for studying ecological open steady state systems. A single long blade of *Sagittaria* with its encrusting mat of aufwuchs was placed in the long glass tube of the apparatus pictured in Figure 6 below. Silver Springs water was circulated thus simulating the natural condition. After a time interval some of the 650 cc of water volume was tapped and tested for changes in oxygen, carbon dioxide and nitrate.

The first conclusion was that in spite of all the light sources in the laboratory which could be brought to bear, the aufwuchs micro-community normally adjusted to outdoor light intensities rapidly used up the oxygen supply and died. It has not yet been possible to get the production up over the community compensation point which is very high because of the heterotrophic as well as autotrophic components.

It was possible, however, to show that nitrate is rapidly fixed by some components in the community even in the dark during wholly respiratory metabolism. This experiment helps to confirm the dark uptake of nitrate found in black bell jars in the field and the slight decrease of nitrate from the boil downstream both in the day and at night. In 5 replications, .37 ppm decreased to .23 ppm in 1 hr and nitrate was not detectable after 6 hrs. "Silver" water standing in glass bottles loses nitrate at a rate of about .2 ppm per month.

Fig. 6. Aufwuchs Microcosm Flow System

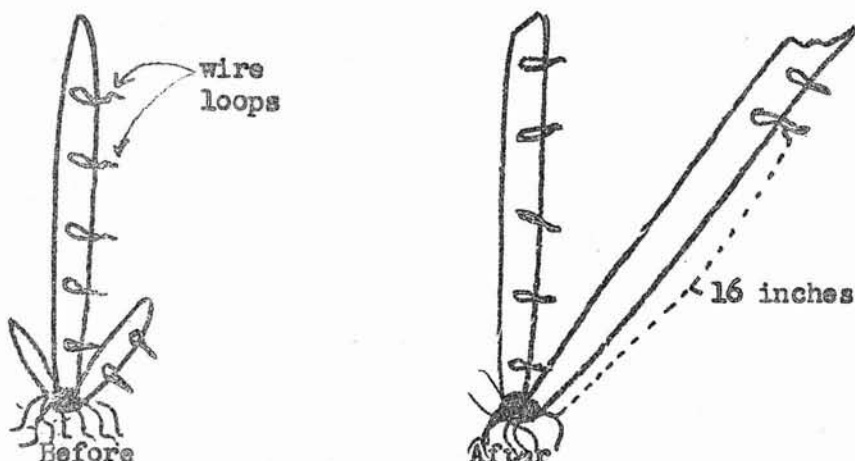


## F. Aufwuchs Succession

The rates of growth and succession of aufwuchs have been measured on slides submerged in the spring and by a count of distribution of plants and animals along the long *Sagittaria* blades. Since *Sagittaria* blades grow from the bottom, it has been possible to measure their growth rate as a means of determining the age of the attached aufwuchs at any place on the blade. The distance from the base of the plant indicates the time since the succession began.

As shown in Figure 7, the rates of growth of single blades is far from equal. Small wires were inserted in a young blade and an older blade in the same clump. After 26 days one blade had shown a rapid 182% growth pushing the attached wires with the tip whereas the other older blade had hardly grown. Apparently a blade shoots out, and then as the aufwuchs covers it growth ceases and goes into new blades. Thus one gets old and younger blades of nearly the same length next to each other, one being clean, the other being covered with the periphyton community.

Fig. 7. 26 day growth of marked blades of *Sagittaria*  
April 5, 1954



For a whole clump of blades, however, there is an average growth which tends to average out these spurts. Therefore by cutting 50 blades into segments of 2 inches length and placing all the first segments together, all the second segments together, etc, one may relate the attached average aufwuchs to the average rate of clump growth. Knowing the area of the blades scraped in each segment group and knowing previously the percent growth of *Sagittaria* from the planting experiments, one converts length into time and periphyton counts into area estimates. If clumps are in steady state the percent loss at the tip of the clump is the percent growth. A count of the last segments when prorated over the spring area gives an estimate of rate of aufwuchs growth and thus of the components of the typical blade type organisms. As an illustration of these methods a curve of midges versus time and thus also length is shown in Figure 8. Estimates of midge growth rate from this curve are discussed below. Some rough curves of succession on glass slides are given in Figure 9. The irregularities in this last Figure may be due to the positions of the slide boxes in different currents and depths. Further work on this is being carried on by Dr. Yount.

The succession patterns are much like planktonic populations with bacteria first, small algae next, then larger algae, and finally herbivores and carnivores as something of a pseudo-climax is attained. Thus one has continual succession in the micro-environments of the overall steady state. Similar microcosms should be looked for in tropical oceanic plankton.



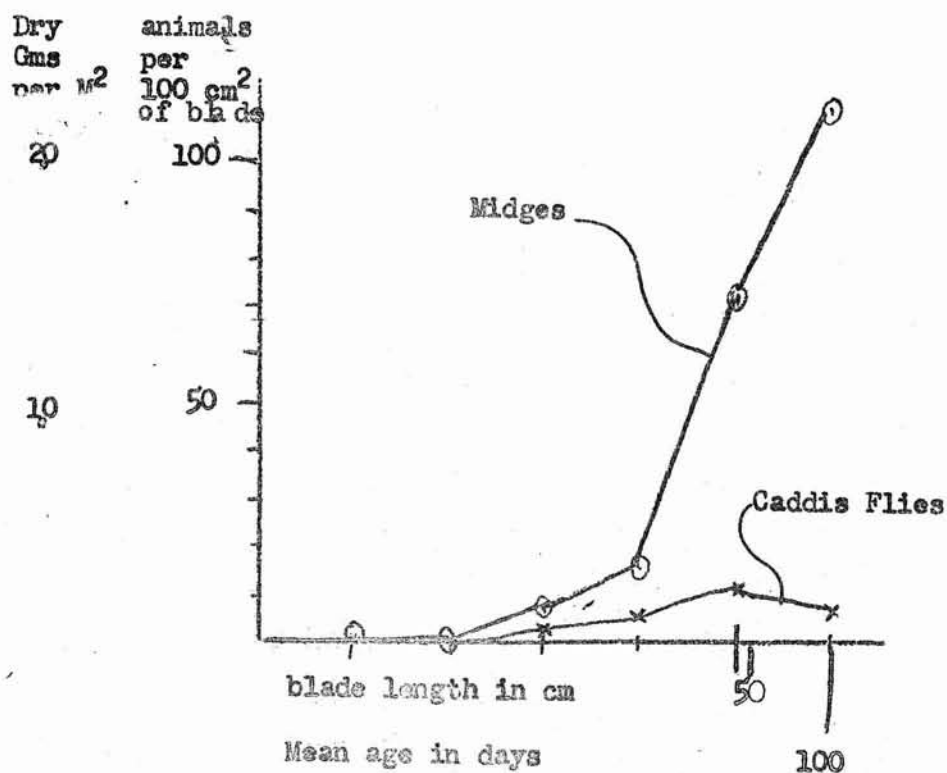


Fig. 8. Succession of Aufwuchs Herbivores on Sagittaria Blades

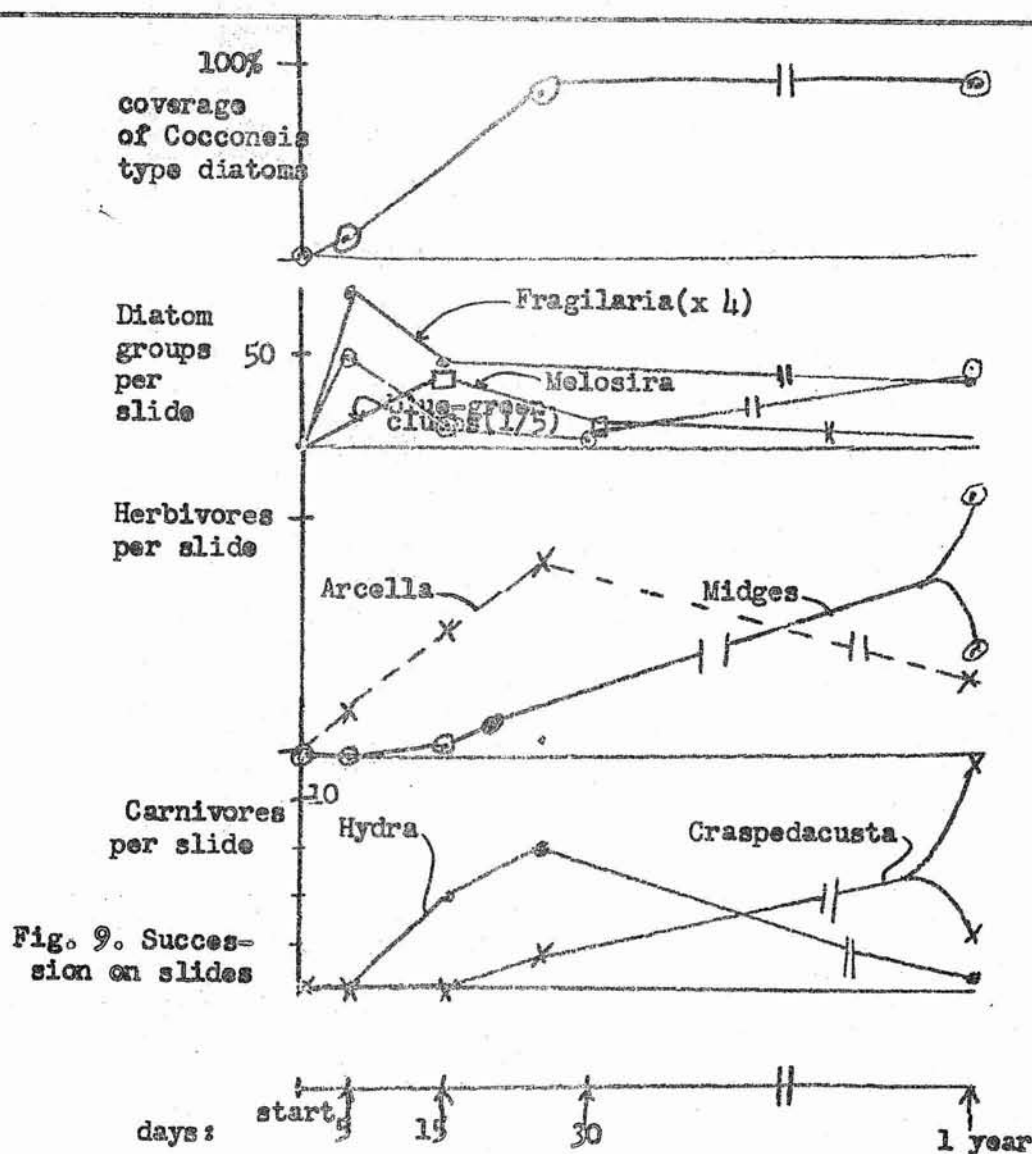
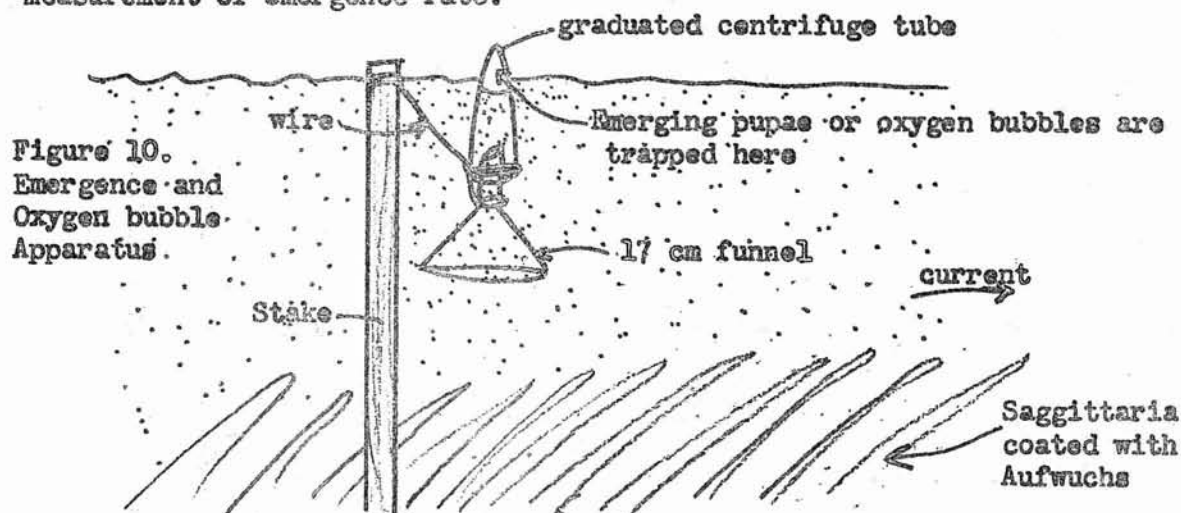


Fig. 9. Succession on slides

### G. Insect Emergence and Oxygen Bubble Measurements

The Very large emergence of midges, caddis flies and other aquatic insects just after sunset has been referred to in previous reports. It has been noted to be intense both on freezing days in winter and hot summer days. Four funnel devices were placed in the spring as shown in Figure 10. Some quantitative counts were obtained from these set ups as given in Table 1. Emergence at dawn is not significant in comparison to the evening outbursts. Rough estimates of herbivore growth rates(net) are calculated below from this measurement of emergence rate.



The same apparatus in Figure 10. is used during the daytime to catch the bubbles of oxygen which are observed to form in the Aufwuchs and then rise to the surface without completely dissolving. This loss of oxygen is a source of error in the production measurements that causes an underestimation of the total production. By arranging the tubes exactly at the water surface, the volume of the bubbles can be converted into a rough weight since the bubbles are at atmospheric pressure. It seems likely that these bubbles are primarily oxygen as 24 hour measurements show a maximum effect at time of maximum photosynthesis. See Table 2.

Table 1 Insect Emergence in Silver Springs  
in apparatus of Fig. 10.

Place	Distance from shore	depth	Date	Time	Midges	Caddis Flies
14 ft.		1.5 ft	May 20	7:30--12:00 p.m.	9	5
			May 28	6:00--11:00 p.m.	1	1
25 ft.		2. ft.	May 20	7:30--12:00 p.m.	8	2
			May 28	6:00--11:00 p.m.	2	1
			May 13	8:20--2:42 p.m.	15	2
40 ft. Station 1	4 ft.		May 20	7:30--12:00 p.m.	5	2
Station 1			May 28	6:00--11:00 p.m.	3	5
Station 2	4 ft.		May 28,	6:00--11:00 p.m.	0	2
Mean					5.4	2.4

Table 2. Bubbles Reaching the Surface in Silver Springs, 1954

Time	Date	Bubbles in cc.	Time Lapse in Hrs.	CC/Hr.
NIGHT: 8:20--2:42 a.m.	May 13-14	0	6.3	0
6:00--11:00 p.m.	May 28	.6 .1 .2 .1		
	Mean	<u>.2</u>	5.0	.04
7:00--3:00 a.m.	May 23-24	0 0 0 .1		
	mean	<u>.025</u>	8.0	.0031
DAY: 4:45--9:30 a.m.	May 23	.1 2.7 .5 .2		
	mean	<u>.9</u>	4.7	.19
2:20 p.m.--4:05 p.m.	May 6	.42	1.7	.25
9:30 a.m.--3:45 p.m.	May 23	2.6 3.1 12.0 3.2		
	mean	<u>5.2</u>	6.2	.83
4:00--7:00 p.m.	May 23	.1 .9 3.1 .1		
	mean	<u>1.1</u>	3.0	.37

## H. Herbivore Production Rates

From data in previous paragraphs some rough estimates can now be made as to the production rates of the dominant herbivores such as were listed in previous progress reports. Several methods are used as follows:

1. From the estimates of midges at the tips of Sagittaria blades in Figure 8 and from the average percent Sagittaria growth of 1%/day from Figure 1 One computes the rate of midge growth necessary to keep up with tip loss in a steady state. This is an underestimation as it does not include early emergence and losses to predation in the middle sections of the grass blades.

2. A few cages of Pomacea and Viviparus snails were maintained with an abundance of food and volume measurements before and after a month growth period. These estimates are underestimates since the snails used were already of moderate size and past the more rapid juvenile growth stages.

3. From the section G above on insect emergence the growth rate necessary to balance the emergence in steady state was determined using .002 gms dry per emerging individual. This figure should probably be added to the Tip-loss figure in method #1 above.

4. From the estimates of standing crop biomass of small invertebrate herbivores in previous reports one can obtain the total respiration using a rough figure for stream invertebrates of .8 cc/gm/hr. Then if growth of animals is about 10% one may get a rough figure for herbivore production.

With these methods some herbivore production estimates are given in Table 3. None of the estimates are entirely satisfactory although the order of magnitude is indicated.

Table 3. Some Estimates of Herbivore Production

Method	Measured Quantities	Production gms/M <sup>2</sup> /Yr.
Blade Tip loss method(#1)	22 gm ridge/M <sup>2</sup> plant surface 25.5 M <sup>2</sup> plant surface/M <sup>2</sup> spring .26 M <sup>2</sup> plant growth/M <sup>2</sup> spring/day (1% blade growth/day)	2190
Snails in Cages method (#2)	6% volume increase/Month Viviparus 1.7% volume increase/Month Viviparus 27% increase/month Pomacea Mean: 11.6%/month; 12 gm/M <sup>2</sup> biomass	17
Insect emergence method (#3)	7.8 individuals/229 cm <sup>2</sup> /day .002 gms/individual	196
	Total of Insects and Snails	<del>22</del> 2403
Assumed <sup>10%</sup> efficiency and .8 cc/gm/hr(method #4)	32.4 gms/M <sup>2</sup> herbivore standing crop	30.

#### I. Carnivore Production Rates

In the fishery biology study described below a few recaptures give some minimal estimates of growth rates of fishes. The average growth rate is about 25%/yr. If the standing biomass is about 7.3 gms/m<sup>2</sup> fish the production is around 2 gms/M<sup>2</sup>/yr. This figure does not include the main stumpknocker populations. Satisfactory biomass estimates of these fish have not been completed. These estimates based on large tagged fish are probably much too low. If 7.3 gms/M<sup>2</sup> fish had a metabolic rate of about .07 cc/gm/hr and an efficiency of 10% the fish growth rate would be .6 gms/M<sup>2</sup>/yr. Considerably more work is required on the higher trophic levels to establish the approximate production and efficiency.

# J. Pyramid of Metabolism, Direct Measurement of Bacterial Metabolism

Even though production rates of all trophic levels are not yet satisfactorily determined, it is instructive to calculate metabolic rates by trophic levels using some literature values of metabolic rate multiplied by estimates of standing crop.

Primary production figures are taken from previous reports. The metabolism of the herbivores is taken as .8 cc/gm/hr with a biomass of 32.4 gms/M<sup>2</sup>. Carnivores are taken as .07 cc/gm/hr with 7.3 gms/M<sup>2</sup> biomass. Top carnivores are estimated from .04 cc/gm/hr with 4.0 gms/M<sup>2</sup> biomass. Rough metabolism figures come from Prosser.

Direct estimates of the bacterial metabolism in the algal gyttja that makes up the community bottom were made with small bell jars placed on the mud surface after the top zone which contained algae was skimmed off. As with larger bell jar experiments described in previous reports, oxygen analyses were made before and after experimental periods under black cloth. Three replications gave oxygen decreases in 95 minutes of 1.27, .75, and 1.84 mg/l. with bell jars 16 cm in diameter and a capacity of 1800 cc. This turns out to be 775 gm/M<sup>2</sup> yr. This estimate does not include the considerable bacterial flora of the aufwuchs which was measured in previously reported work. It is important to note that although much smaller in biomass the decomposer bacteria are more important metabolically than the regular herbivores.

The various rough estimates of metabolism by trophic level are summarized in Figure 11 below: This is thus a first attempt to assign values to the metabolism diagram previously presented.

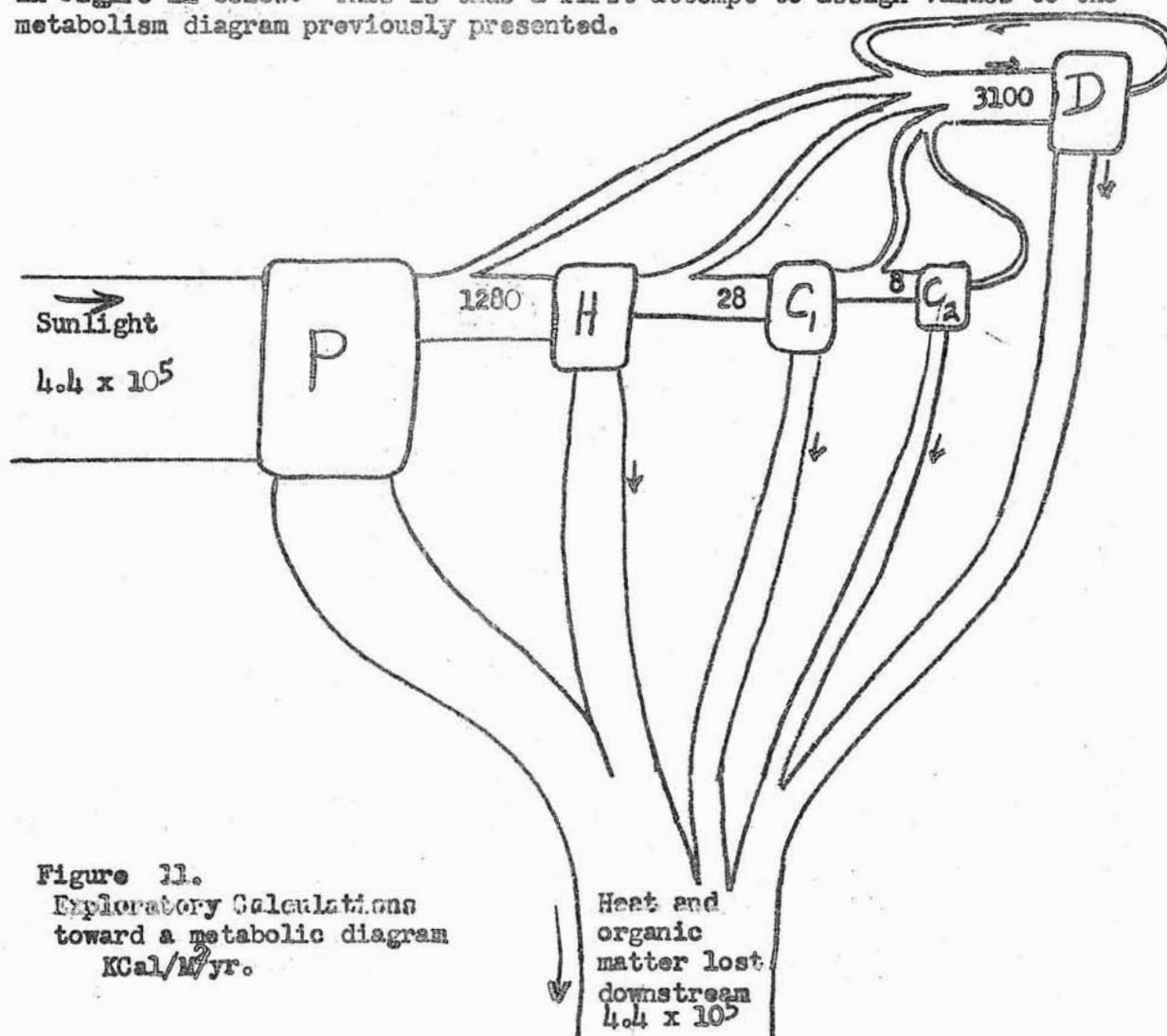


Figure 11.  
Exploratory Calculations  
toward a metabolic diagram  
KCal/M<sup>2</sup>/yr.

# K. Diurnal pH Curve by Measurement and Dye Nomogram from Carbon Dioxide

In Figure 12. below is given another days determination of production with oxygen and carbon-dioxide curves such as have been given in previous progress reports. This time water samples were brought back to the laboratory and the pH determined with a Beckman model G. The maximum time of 24 hours is not so serious in these low organic matter waters as would be the case with most natural waters. The carbon dioxide values were then converted into calculated pH values from the known alkalinity. The measured and curve calculated with the Dye nomogram are both shown below:

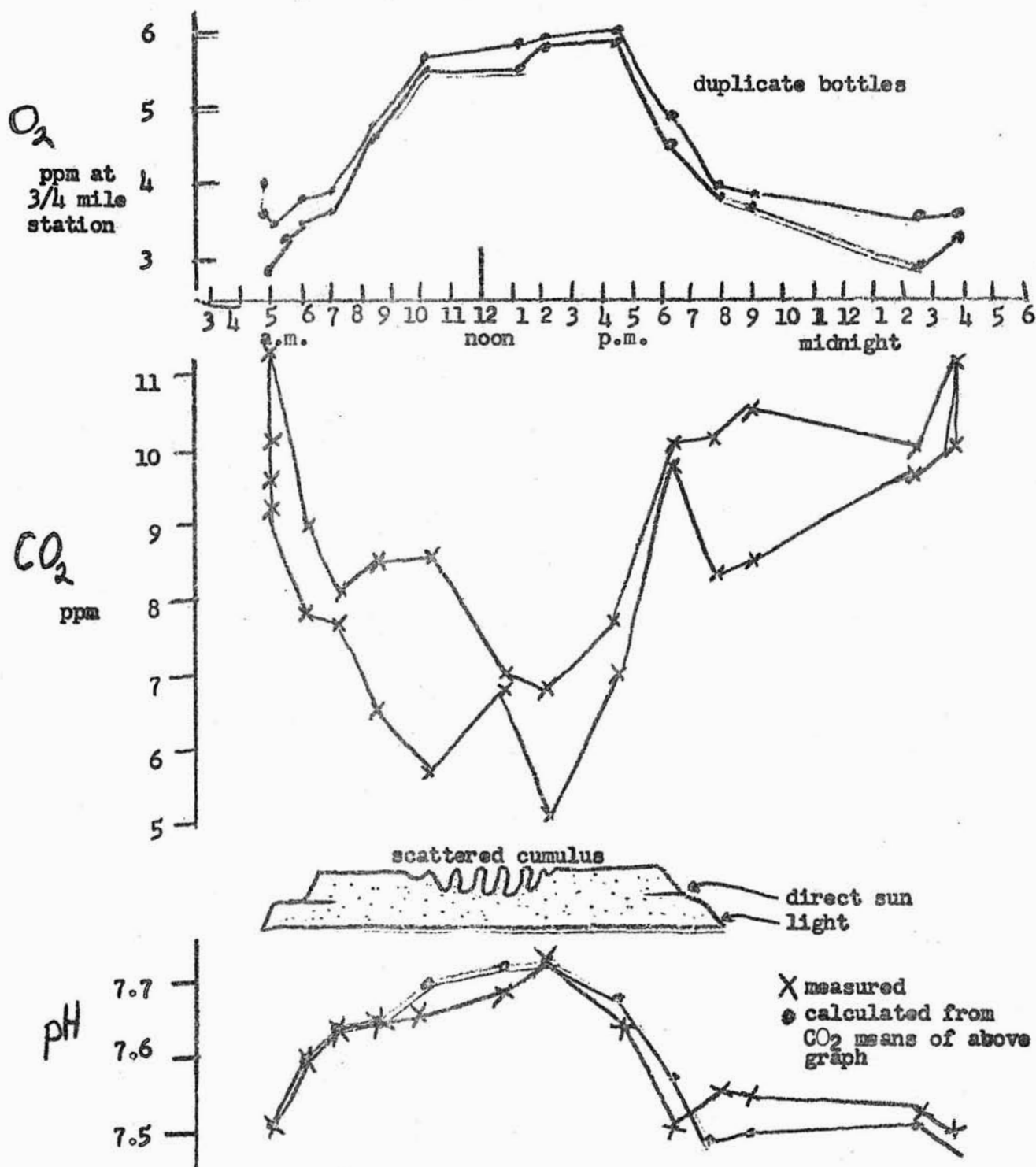


Figure 12. Diurnal Curves for 3/4 mile station May 23-24, 1954



## COMPARISON OF AN ENIWETOK CORAL REEF COMMUNITY WITH SILVER SPRINGS

In the summer of 1954 H.T. Odum and E.P. Odum (Univ. of Georgia) made a study of the productivity of a windward reef on Eniwetok Atoll primarily under sponsorship of the Atomic Energy Commission and the University of Georgia by means of a contract extension of a project directed by E.P. Odum. This endeavor was also supported in part by the Navy and indirectly by the techniques used in the Silver Springs work.

One main purpose was a comparison of the characteristics of Silver Springs and the Japtan inter-island reef. The 80 page report on the Eniwetok study has just been completed and submitted to the AEC prior to publication. A few of the conclusions which are significant to the understanding of the Silver Springs community and steady state systems in general may be listed as follows:

1. Both communities are very efficient, the coral reef being 6%.  
(of visible light energy reaching average community depth.)

2. Both are immensely fertile. The coral reef with production rates above 75,000 lbs. glucose per acre per year is among the highest on earth. Silver Springs is more productive in summer months but has a lower annual production.

3. Both systems are essentially autotrophic in primary trophic level. (John Teal, Harvard Univ., is working on productivity of a small spring whose primary production source is not light but allocthonous organic matter.) Sargent and Austin's pioneer studies on reef productivity were in general confirmed. Glass slides down 3 weeks in both Silver Springs and Eniwetok yield coatings of algae rather than fouling communities found in inshore oceanic waters.

4. The pyramids of standing crop of Eniwetok and Silver Springs are surprisingly similar suggesting that in similar current situation a similar ratio of big slow producers and little fast producers may be necessary to maintain optimum structure. Note the comparative pyramids in Figure 13 and in previous progress reports. Algae in calcareous substrates was estimated with a chlorophyll extraction method.

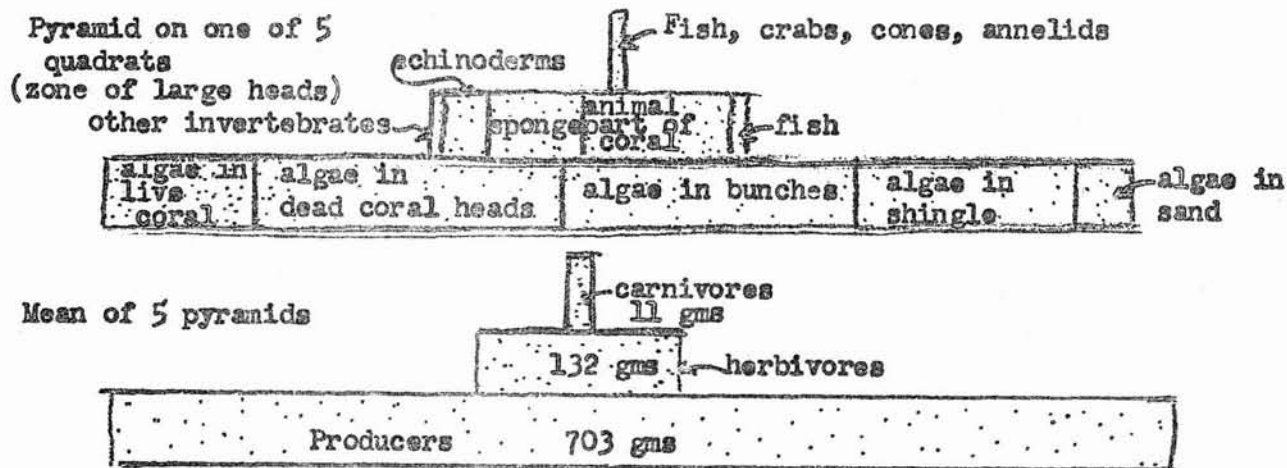


Figure 13. Pyramids of live biomass (non calcareous) on Eniwetok--Japtan inter-island reef; Figures in dry gms/m<sup>2</sup>

5. Both communities are close to a steady state with production balanced by respiration in the coral reef within the limits of accuracy of the measurements made. In Silver Springs there is always a contribution of the upstream organic matter to the downstream communities which the reef does not have. (except to a very small extent) Curves showing production and respiration are given in Figure 14. along with previous data of Sargent and Austin

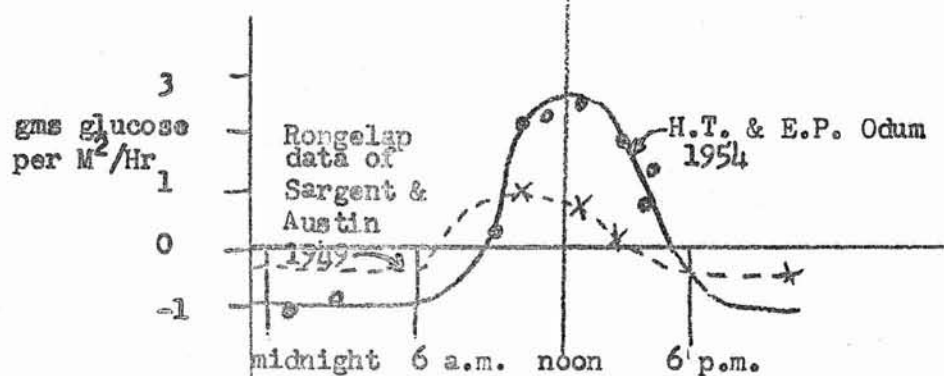


Figure 14. Diurnal Curve of Production Measured with the Upstream-downstream flow method on Eniwetok Windward Reef

6. Both systems are known to have been at least roughly in steady state balance for long periods of time and it is important that contrasting systems tend to achieve the same trophic structure and characteristics in steady state suggesting similar basic laws of behavior as discussed in the theoretical section below.

7. It is further surprising that similar high efficiencies are achieved by a very high nutrient flow in Silver Springs and by a very low nutrient condition in the coral reef. Thus if the proper adapted organisms are available the particular deficiencies of possible environmental limiting factors may be circumvented by a community by expending some part of its energy in mechanisms for conserving the limiting factor so that it is no longer limiting except that it maintains a small energetic tax on the overall system. In the coral reef case this is the conservation of nutrients in the calcareous skeletons.



## PLANT COMMUNITY STABILITY DURING 3 YEARS

by H. T. Odum

In 1951 maps were made of the distribution of plants in 40 springs. One of these, Fanning Spring, was reproduced in the first progress report.

In the following report by Dr. Natelson, entirely independent maps are reported, made 3 years later in 6 of the same springs without having seen but one of the previous maps. The comparison of the earlier maps with the later maps is very indicative of the degree of stability in these chemostatically and thermostatically regulated natural communities. It is apparent that in general the same species dominate after three years although the exact positions of the various patches shifted. It should be remembered from the work in Silver that the higher plants have a turnover of between one and 10 times a year so that there has been ample time for marked changes. This is further evidence along with the previously reported work on algae and insects that conditions are much more stable than usually found in nature. This is not to imply that pulses and changes have not occurred in some springs; in some springs more affected by surface water, there is also a known variation of chemical conditions.

## Standing Crop and Community Survey of Submerged Vegetation On Seven Springs

By Delle Natelson

In the first semi-annual report of this project in January, 1953, Dr. John H. Davis presented figures on the standing crops of four springs and their coastal runs and called attention to changes in density and composition of the vegetation, some of which were correlated with changes in turbidity and chlorinity of the water. This is a report on work intended to continue and extend the above studies. The present investigation, which began in September, 1954, has for its subject both the quantitative features of the standing crop of large submerged aquatic plants in some springs and their runs and the qualitative composition of their prevalent communities.

An investigation of the submerged vegetation in Wisconsin lakes revealed no discrete recurring communities. Instead, there occurred a pattern of continual change of community composition along a gradient complex of environmental factors (Natelson, D., The phytosociology of submerged aquatic macrophytes in Wisconsin lakes. Ph.D. Thesis, University of Wisconsin, 1954). One of the principal aims of the present study is to determine if such a situation exists in the aquatic vegetation of Florida, and if so, what is the pattern of vegetation here. A knowledge of the pattern, referred to as "vegetational continuum", can be used in constructing a classification system for the communities and facilitates correlations among vegetation and environmental factors. The Florida studies here reported are based upon methods used in the Wisconsin investigation.

Each run was sampled at several stations scattered along the length of the river. Some subjectivity was used inasmuch as care was taken to sample characteristic, rather than atypical or disturbed areas, but selection of stations was otherwise objective, with two exceptions: 1) in some instances, for comparison purposes, an attempt was made to sample at the same station used by Dr. Davis or Mr. Sloan (Sloan, Wm., The distribution of aquatic insects in two Florida Springs, M.S. Thesis, Univ. of Fla., 1954); 2) stations at Salt Springs run were located regularly at two-mile intervals since the water was too turbid for reliable selection.

The sampling transects made across the river frequently traversed two or more obviously different communities and such stations were divided into substations. Each of the latter were sampled individually, so that the data could be used for general community analysis as well as for standing crop and species composition estimates for each river. For the latter purpose, the several substations at each station were weighted according to the area of the station which they occupied, and they were then combined. This technique was also used for pools where a mosaic of communities occurred.

Substations or stations with homogeneous vegetation will be referred to as stands. Each stand was sampled by 5 to 25 quadrats, according to the homogeneity of the vegetation and/or the area of the stand. The quadrat was a heavy wire frame one square foot in area. With the aid of a face mask, the rooted plants within the quadrats were uprooted and brought to the surface. But sometimes, where the depth and substrate were suitable, a rake was used to denude one square foot of the bottom (estimated), instead of uprooting by hand.

To determine the volume of the plants, the displacement of water by the plants removed from the quadrats was measured using the method described by Dr. Davis (cited above), and an average volume per square foot was calculated for each stand. Since the specific gravity of submerged plants is close to one, these figures were used as an estimate of the wet weight of the plants. The percentage cover of the vegetation in each section of river was multiplied by the weight of the vegetation of the stand sampled in that section, and the results were converted to lbs./acre wet weight for each section. Wet weight of the vegetation in each section was weighted by the estimated relative area of the section in the river and the resulting figures were combined to produce an estimate of the average wet weight/acre in the river.

The percentage of volume contributed by each species was estimated for each quadrat, and an average was obtained for each stand. These figures were then weighted by the percentage cover and percentage area of each stand in the river, in the same manner as described above for the combined wet weights. Thus the percentage of the wet weight of plants in the river contributed by each species was obtained. The percentage of water content of each species as previously determined by Dr. Davis (unpublished data) was used to obtain the dry weight contributed by each species to the average dry weight/acre for the river.

Estimates of total standing crops, both as wet and dry weight, and the percentage of the total dry weight which was contributed by each species are presented in Table 1.

Figures 1 and 2 illustrate the spring-river systems whose standing crops were summarized in Table 1, and the locations of stations and the area estimated as representative of each station are shown.

Across a river, from shore to shore, different communities often occur within small areas, even at the same depth. Frequently, an environmental correlation is obvious, e.g., different substrates. However, in other situations no reason for the differences is apparent and it is probable that historical factors such as disturbance, availability of propagules, and conditions conducive to clone formation were largely responsible for the non-uniformity of the vegetation.

In contrast, a regular trend in vegetation change downstream occurs in some rivers, superimposed upon the more random localized variability. In this investigation, such trends were noted in the springs with coastal runs. In Weekiwachee River, Chara occurred near the head, often in great density, but was not found in the middle or lower parts of the river. Ceratophyllum demersum likewise occurred in greatest abundance near the head, but extended much further downstream than Chara. As Chara decreased in importance, Najas guadalupensis, which was absent from the upper part of the river, appeared and rapidly became the most abundant species. Sagittaria was more prevalent in the upper part while Potamogeton pectinatus and Vallisneria neotropicalis were apparently restricted to the lower part of the river.

Chassahowitzka River was similar to Weekiwachee River in some of its vegetational features. Sagittaria was most abundant near the head while Vallisneria neotropicalis, Najas guadalupensis, and Potamogeton pectinatus reached their maxima in the lower part of the river.

Such trends were not apparent in Homosassa River, except for the occurrence of large amounts of filamentous green algae in the middle section of the river although it was rare in the upper and lower regions. However, a distinct change in the character of the vegetation occurred near the Gulf where tidal waters introduce salinity. There Potamogeton pectinatus and algae of marine type occurred, while the common upstream species were rare.

These three rivers run from their head springs to the Gulf and thus contain a gradation in chlorinity, as was shown by data presented by Dr. H. T. Odum in the January, 1953 report of this project. Tables 2 to 5 show the qualitative changes in vegetation which occur in some instances from the head of a river to its mouth, and also show how equally great or even greater variation often occurs among substations at the same general location. Thus it seems that excluding brackish waters, changes in chlorinity are probably not as much the cause of community differences as are the changes in substrate and turbidity.

Changes in community composition in the Salt Springs run, which does not flow into salt water but into Lake George, showed no consistent trends, except for the fact that Potamogeton pectinatus was the most abundant species in the pool area and the beginning of the run, and was absent or rare elsewhere.

Hart Springs run had essentially the same plant composition throughout its short length.

Sources of error in this work fall into two principal categories. The first results from the mosaic arrangement of the communities which is revealed by Tables 2 to 5. Because of this, the error can be considerable when the standing crop or



species composition estimate for a river is derived from a fairly small number of stations. The second source of error arises from the necessity for estimating the plant cover of each section of the river and the extent of the section represented by each stand.

In addition, there are small errors which result from difficulties in sampling, i.e., the current effects which often bend the vegetation horizontally and do not permit the quadrat to be dropped over the top of the plants so that one square foot of bottom can be denuded. However, these errors may often compensate for each other. For example, the excess weight contributed by soil particles, which usually come up with the roots, is to some extent compensated for by the fact that frequently a large part of the root system is left in the substrate.

An idea of the relatively small size of error or variability in results obtained is shown by a comparison between Dr. Davis' results (cited above) and those of this investigation.

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	<u>Lbs./acre</u> <u>Dry Wt.*</u>	<u>Lbs./acre</u> <u>Dry Wt.#</u>	<u>Error</u>
Weekiwachee Springs and River	3941	4686	16%
Chassahowitzka Springs and River	4620	3667	26%
Homosassa Springs and River	4000	3774	6%
		Average error	=16%

\*From Dr. Davis' data.

#From the present work, converted from wet weights by conversion factors.

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This comparison of results of work done entirely independently by two persons leads to the conclusion that standing crop estimates are relatively good first approximations of the productivity of spring-river ecosystems. However, it should be emphasized that it has not been possible to determine from this study what part of the differences between the two estimates for the same river is attributable to chance errors in sampling and which to possible actual differences in the vegetation when the estimates were made.

The pools of some of the spring boils were mapped and are shown as diagrams in Figures 3 to 7. The areas of similar vegetation (stands) in each were delineated and the communities analyzed in a manner similar to the substations of the runs. Each species is represented by a symbol whose frequency in each stand on the map indicates its relative importance in the community as determined by frequency calculations and volume measurements or estimates.

These maps illustrate how several different communities often occur within a small area. Work on communities will continue through the spring of 1955 and probably will shed light upon some of the community and site relationships.

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Notes:

1) The species mentioned in this report are listed below with their taxonomic authors:

Ceratophyllum demersum L.

Ludwigia natans Ell.

Najas guadalupensis (Spreng) Morong

Potamogeton illinoensis Morong

P. pectinatus L.

Rorippa sessiliflora (Nutt.) A. Hitchc

Vallisneria neotropicalis Marie-Vict.

2) The locations and descriptions of the springs and their rivers discussed here are given in Ferguson, G.E., C. W. Lingham, S. K. Love, and R. O. Vernon, Springs of Florida, Geological Bulletin No. 31, State of Florida Department of Conservation, Tallahassee, 1947.

Table 1. Estimate of total standing crop and percentage contributed by each species in 5 springs and their rungs.

	Week1.	Chassa.	Homo.	Salt	Hart	Fanning
Date	11/8	10/23	10/5	10/1	10/3	10/7
Wet wt. lbs./acre	35272	27495	37926	20137	17977	6684
Dry wt. lbs./acre	4686	3437	3774	2045	1814	802

Percentage of the total dry weight which was contributed by each species:

Algae (filamentous)		.8	3.3			20.1
Anacharis canadensis		.1				
Cabomba sp.					4.8	
Ceratophyllum demersum	9.0	6.5	22.9	16.5	10.1	1.3
Chara spp.	19.3					
Hydrocotyle spp.						7.9
Ludwigia natans					1.1	27.6
Najas guadalupensis	37.6	35.2	40.9	66.4	84.2	
Potamogeton illinoensis		2.9				
P. pectinatus		13.6	9.1			
Rorippa sessiflora						2.2
Sagittaria spp.	29.1	33.8	.7			
Vallisneria neotropicalis	1.8	4.3	22.4	11.0		36.2
Others	3.3	3.3	.6	6.1		4.3

Table 2. Homosassa River: Composition and standing crop of vegetation at the substation community level.\*

Species	Importance**									
	A	B <sub>1</sub>	B <sub>2</sub>	B <sub>3</sub>	C	D <sub>1</sub>	D <sub>2</sub>	E	F	G
Algae (filamentous)		13	20	64	6				32#	35#
Ceratophyllum demersum		39	18	3	29	3	33	19	3	
Najas guadalupensis	56	32	18	28	30	64	48	40		
Potamogeton pectinatus	8		2	2	14			23	67	65
Sagittaria sp.		12								
Vallisneria neotropica	37	3	42	3	21	33	19	18		
Others		2								
lbs./acre wet weight	207	585	585	10	717	604	604	84	95	20

\* Communities represented by the same letter and different subscripts are substations at the same location.

\*\* Importance is expressed by  $\%F \times 2\% V/3$ , where  $\%F$  = relative frequency and  $\%V$  = relative volume as measured by displacement of water.

# Algae of marine type

Table 3. Chassahowitzka River: Composition and standing crop of vegetation at the substation community level.

	Importance											
<u>Species</u>	A	B	C <sub>1</sub>	C <sub>2</sub>	D <sub>1</sub>	D <sub>2</sub>	E <sub>1</sub>	E <sub>2</sub>	F	G <sub>1</sub>	G <sub>2</sub>	
Algae	3		20	7	10	1	10	35	2			
C. demersum	2				8	3			21			
N. guadalupensis	16			15		1	10	26	44	52	82	
P. illinoensis					6	15	8	11				
P. pectinatus				37		22	6	8	29	48		
Rorippa sessiflora	1											
Sagittaria sp.	72	100	80	41	76	59	54	9				
V. neotropicalis	7						13	10	4		18	
lbs./acre wet weight	509	160	150	210	340	330	204	120	320	952	150	



Table 4. Weekiwachee River: Composition and standing crop of vegetation at the substation community level.

<u>Species</u>	<u>Importance</u>						
	<u>A</u>	<u>B</u>	<u>C</u>	<u>D</u>	<u>E</u>	<u>F</u>	<u>G</u>
Algae	7	5					
Ceratophyllum demersum	49	45					
Chara sp.	24	49					
Ludwigia natans		9					
Najas guadalupensis			100	59	1000		44
Potamogeton pectinatus						42	25
Sagittaria sp.	20	37		5		33	
Vallisneria neotropica				37		26	31
Lbs./acre wet weight	675	320	180	440	180	1	180

Table 5. Salt River: Composition and standing crop of vegetation at the substation community level.

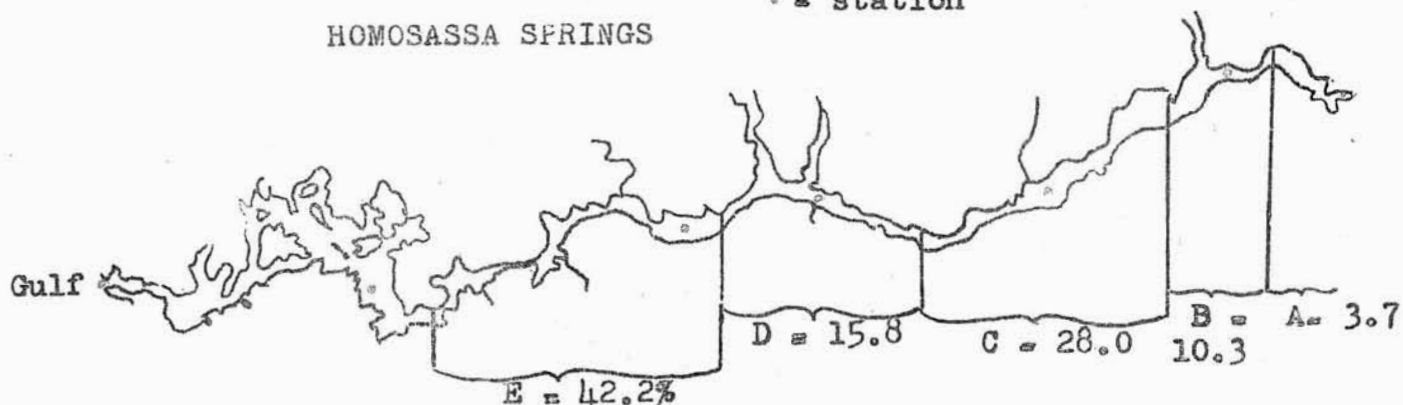
<u>Species</u>	<u>Importance</u>									
	<u>A1</u>	<u>A2</u>	<u>A3</u>	<u>B</u>	<u>C</u>	<u>D1</u>	<u>D2</u>	<u>E1</u>	<u>E2</u>	
Algae	4	11	4	16		8				
Ceratophyllum demersum				18	21	41	2	4		
Chara sp.							2			
Najas guadalupensis	24	60	23	49	79	51	82	19	41	
Potamogeton pectinatus	56	11	49	2						
Vallisneria neotropicalis	15	18	24	16			14	76	59	
Lbs./acre wet weight	200	200	300	828	193	8	83	230	40	

Figure 1. Locations of stations and section of river represented by each station.

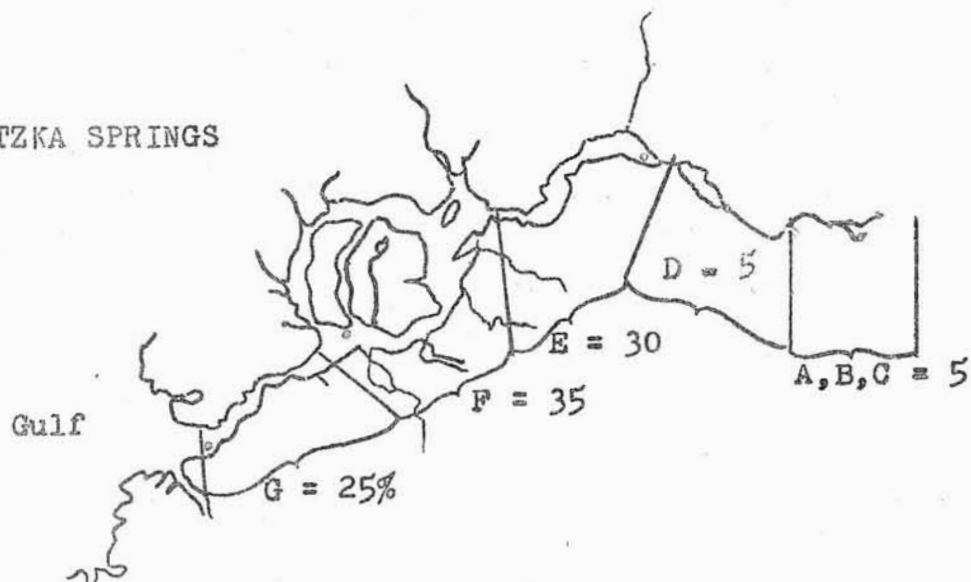
1 inch = 1 mile

• = station

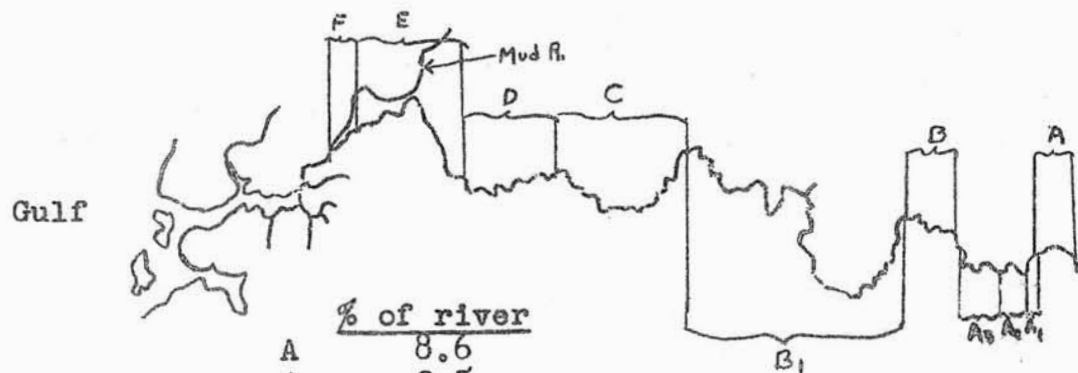
### HOMOSASSA SPRINGS



### CHASSAHOWITZKA SPRINGS



### WEEKIWACHEE SPRINGS



#### % of river

A	8.6
A <sub>1</sub>	2.5
A <sub>2</sub>	7.5
A <sub>3</sub>	8.6
B	3.7
B <sub>1</sub>	25.0
C	18.8
D	6.2
E	16.2
F	2.5

Substations in Weekiwachee River are estimations for sections of the river which were obviously not represented by the sampled stations.

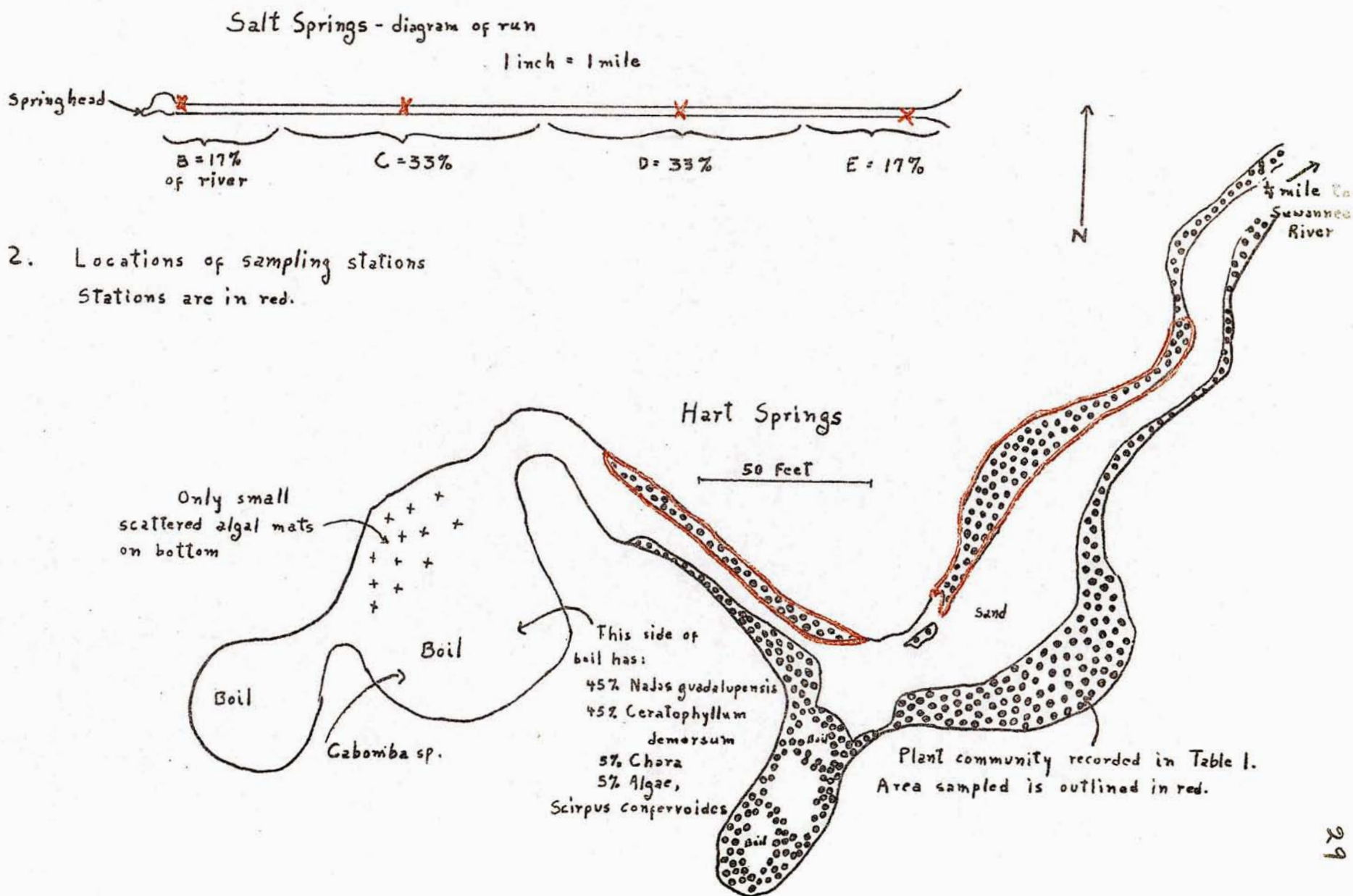


Figure 2. Locations of sampling stations  
Stations are in red.

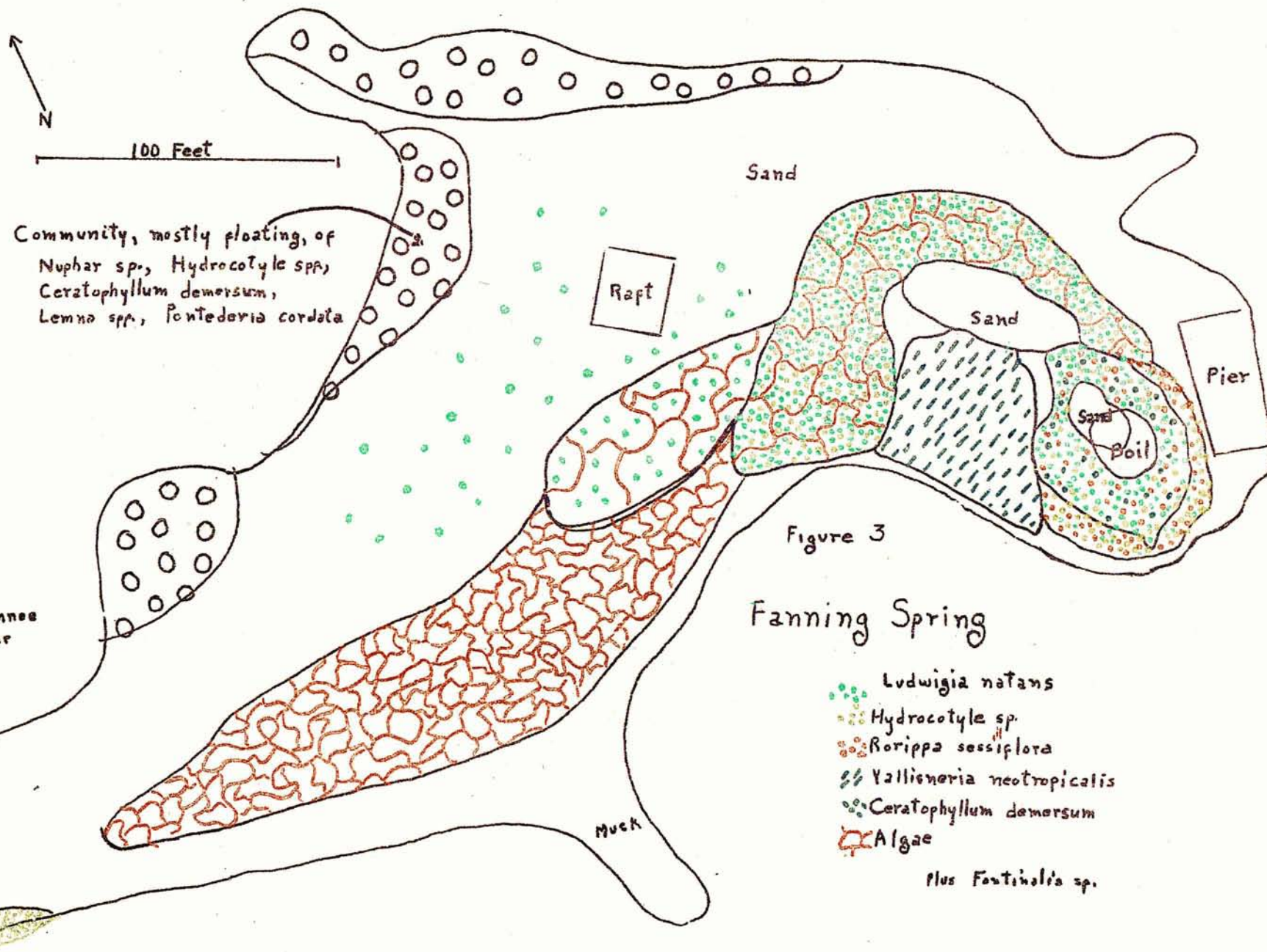
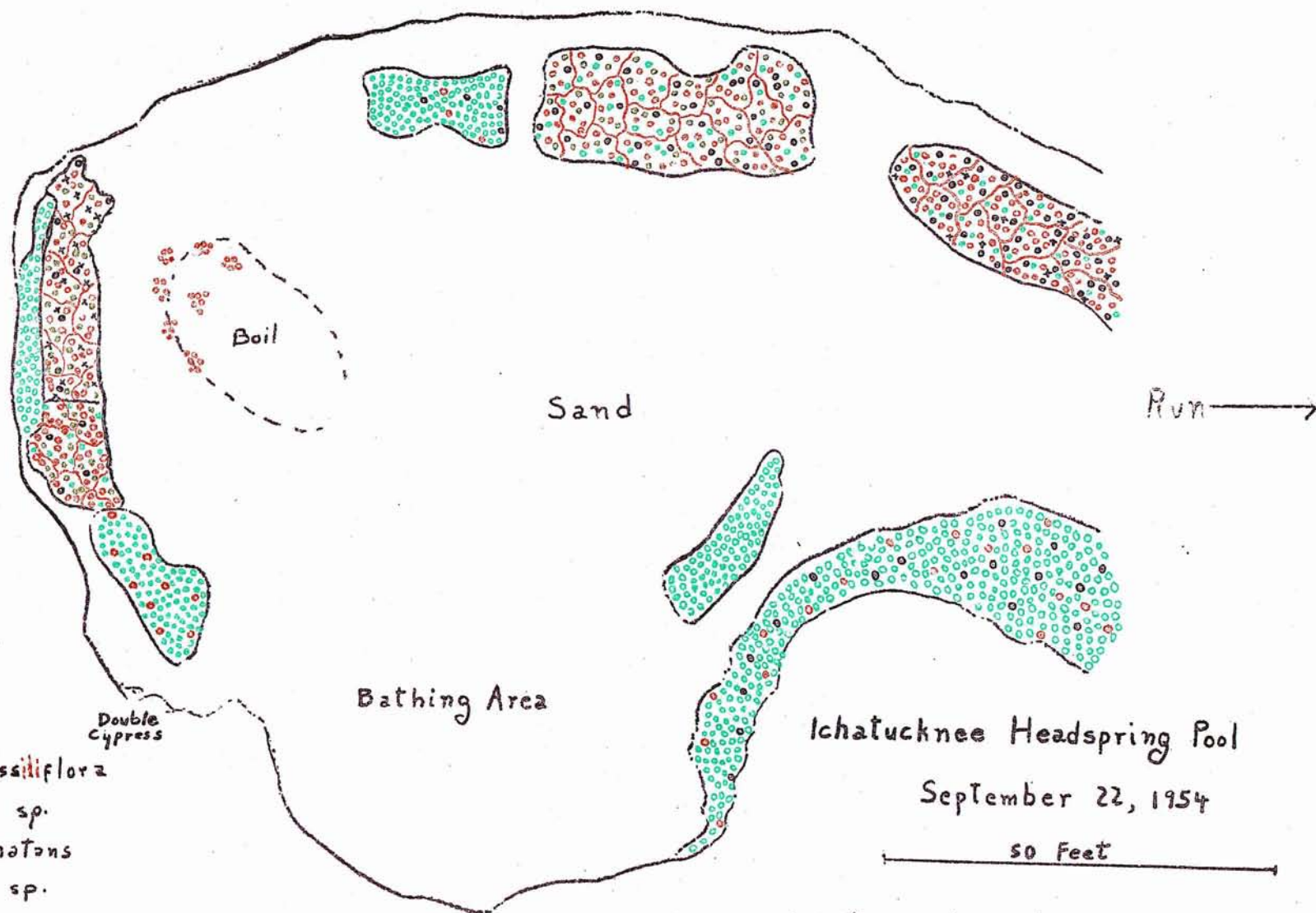




Figure 4

- *Rorippa sessiliflora*
- *Hydrocotyle* sp.
- *Ludwigia natans*
- *Fontinalis* sp.
- *Chara*
- *Najas guadalupensis*
- *Algae*
- *Myriophyllum*



Ichatucknee Headspring Pool

September 22, 1954

50 Feet

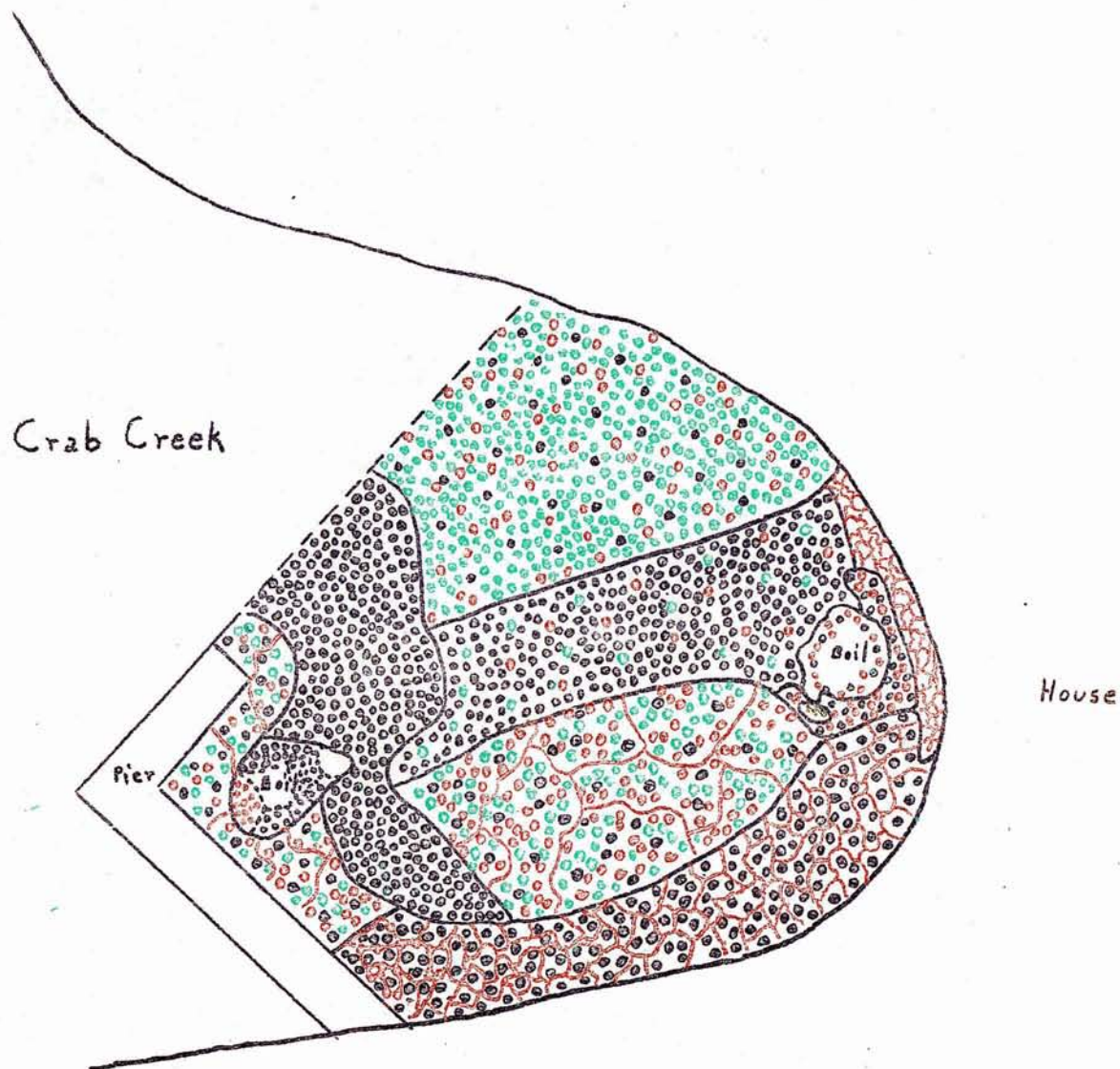
Amounts of each species shown are based upon relative frequency only.

Figure 5  
Crab Creek Pool  
at Chassahowitzka Springs  
October 24, 1954

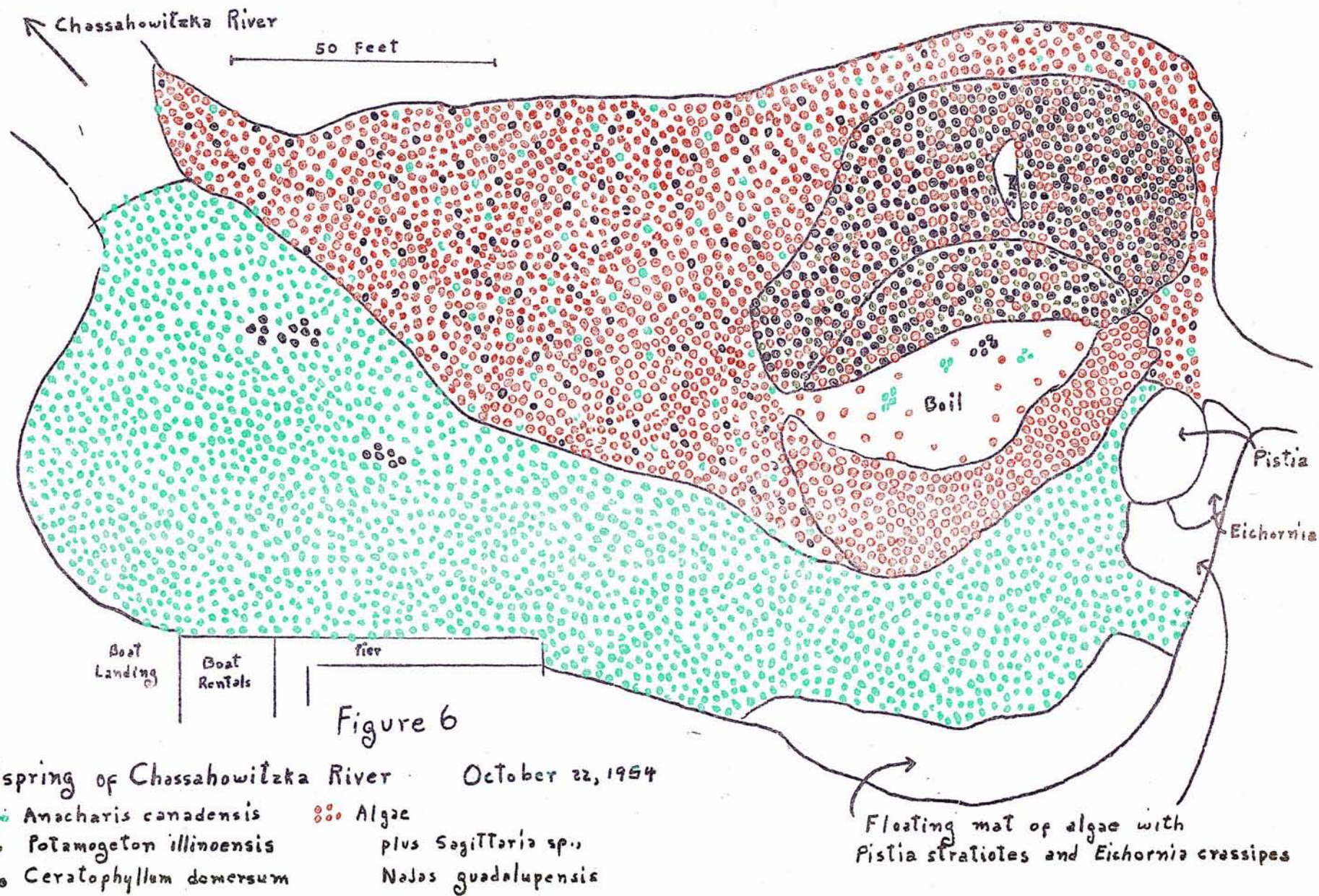
50 Feet

- *Najas guadalupensis*
- *Sagittaria* sp.
- *Vallisneria neotropica*
- *Potamogeton pectinatus*
- Algae
- plus *Ceratophyllum demersum*
- Fontinalis* sp.
- Zannichellia palustris*

← Crab Creek









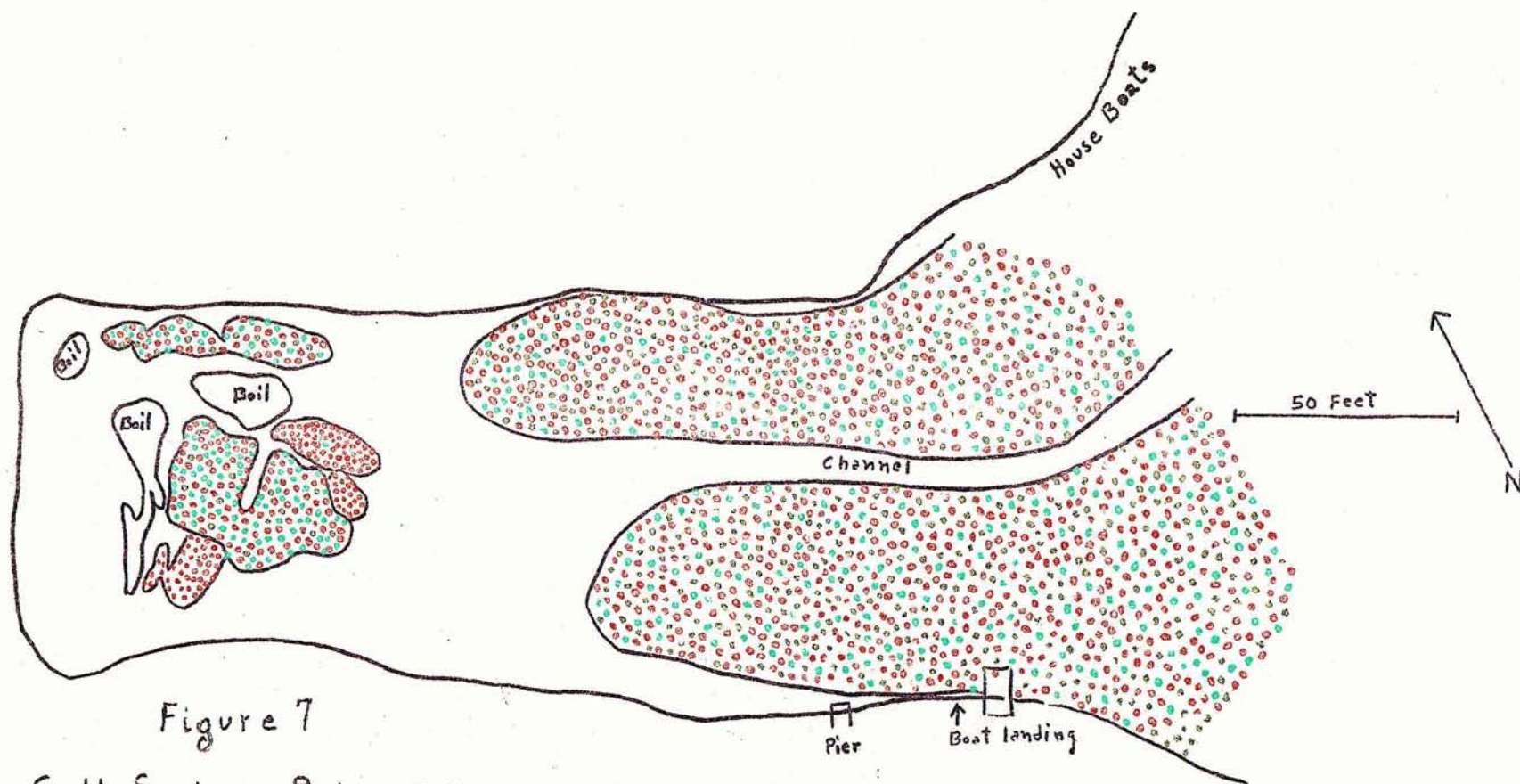


Figure 7

Salt Springs Pool and Upper Run  
September 30, 1954

- *Potamogeton pectinatus*
- *Vallisneria spiralis*
- *Najas guadalupensis*  
plus algae



## FISHERY BIOLOGY STUDIES IN SILVER SPRINGS

By David K. Caldwell, Frederick H. Berry, and Howard T. Odum

A fish tagging program in Silver Springs was begun on March 12, 1954, and has been continued by various workers to date. A total of 19 trips have been made with the assistance of a number of volunteer helpers. To date, 392 fish have been tagged in Silver Springs. Two types of tags have been used. Plastic Peterson disc tags of varying colors and sizes have been used on the larger fish, and small metal clamp tags have been placed on the jaw or opercle of smaller specimens. The latter are numbered, while the unnumbered plastic tags have been used in various color combinations for each fish, or have been used cut to different shapes with the same color combinations. Most of the fish tagged have been Largemouth black bass (Micropterus salmoides) and Stumpknockers (Lepomis p. punctatus), with some other Centrarchids and a few other species. The numbers of each species tagged and the type of tag are summarized as Table 1. As summarized in Table 2, ten fish have been recaptured. Although enough time elapsed between tagging and recapture for some growth to occur, some fish have not shown any increase, and others show an apparent decrease. Whether these growth values are typical or whether an artifact or injury is involved is not yet clear. The bass show the most growth, and all of these specimens are juveniles. It is interesting to note that all recaptured fish were retaken where they were initially caught and tagged.

Regular samples of Stumpknockers (the dominant species) have been taken each month beginning in June, and in March. Length-frequency curves and length-weight curves have been constructed with these. The length-weight ratio does not vary materially from month to month, at least for the sizes measured. A typical weight-length curve is shown as Figure 1. Enough specimens of other species have not been taken for the construction of such curves. Monthly length-frequency graphs for the Stumpknocker do not show any distinct age groups (Figure 2). A very long breeding period is thus indicated. There is also evidence to support this from observations of spawning beds and ripe (or nearly so) adults during most of the warm months. Though an entire winter period has not yet been sampled, evidence indicates that spawning, although rare during this period in Silver Springs, does occur. Individuals with developed gonads were taken on October 15 and on December 15. Also, small specimens were taken during the winter (Figure 2).

Samples of scales have been taken throughout the study and an effort is now being made to determine if these can be used in determining age and rate of growth. This study is primarily being done on the Stumpknocker, though some attempt will be made to study the scales of the other Centrarchids, particularly the bass. Preliminary studies show the presence of rings, but further study is

necessary to determine if these rings represent true annuli. Scales from this constant temperature spring will be compared with scales from the same species from other (non constant temperature) Florida waters, and if possible with scales from northern waters.

A straight line ratio has been shown to exist between standard length and total length for the Stumpknocker. This ratio ( $S.L./T.L. = .79$ ) exists throughout the entire size range for this species as encountered in Silver Springs, and will be helpful in comparing the work done in Silver Springs with that of other workers on the same species in other areas.

Coincident with the fishery work on larger fishes, a general collection of small fishes, invertebrates, and algae has been made for further study of seasonal periodicity of reproduction in this constant temperature environment.

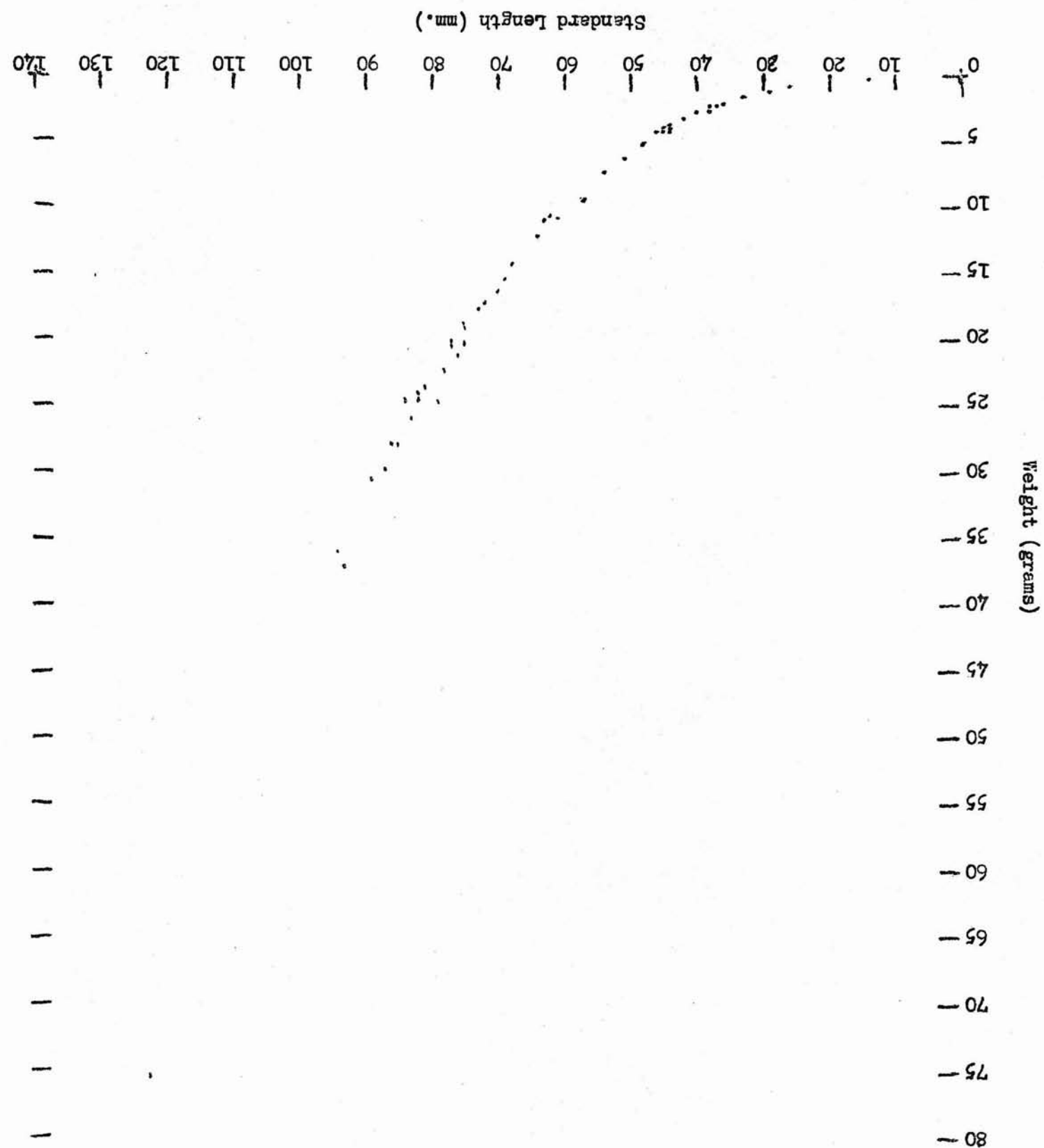
SPECIES	NUMBER WITH METAL TAG	NUMBER WITH PLASTIC TAG	TOTAL
<u>Lepomis p. punctatus</u>	83	147	230
<u>Lepomis macrochirus</u>	12	12	24
<u>Lepomis auritus</u>	3	0	3
<u>Lepomis marginatus</u>	1	0	1
<u>Lepomis megalotis</u>	25	9	34
<u>Lepomis microlophus</u>	1	1	2
<u>Micropterus salmoides</u>	40	19	59
<u>Chaenobryttus coronarius</u>	11	17	28
<u>Esox americanus</u>	1	1	2
<u>Pomoxis nigromaculatus</u>	0	1	1
<u>Lepisosteus platyrhincus</u>	0	3	3
<u>Anguilla rostrata</u>	0	1	1
<u>Erimyzon sucetta</u>	0	1	1
<u>Ameiurus natalis</u>	0	3	3
Grand totals	177	215	392

Table 1. Summary of fish tagged at Silver Springs, Florida, between March 12, and December 29, 1954.

Species	Tag Type	Date Tagged	Date Recaptured	Days Out	St. Len. (mm) When tagged	St. Len. at Recap.	Growth (mm)
<u>Micropterus salmoides</u>	Metal	VI-11-54	IX-24-54	105	124	134	10
<u>Micropterus salmoides</u>	Metal	VII-25-54	X-15-54	82	112	131	19
<u>Micropterus salmoides</u>	Metal	IX-24-54	X-15-54	21	116	115	-1
<u>Micropterus salmoides</u>	Metal	VII-25-54	XI-24-54	122	110	128	18
<u>Micropterus salmoides</u>	Metal	IX-24-54	XII-15-54	82	120	124	4
<u>Micropterus salmoides</u>	Metal	IX-24-54	XII-29-54	96	105	107	2
<u>Chaenobryttus coronarius</u>	Plastic	VI-18-54	X-15-54	119	116	116	0
<u>Chaenobryttus coronarius</u>	Metal	VI-18-54	X-15-54	119	112	117	5
<u>Lepomis p. punctatus</u>	Plastic	VIII-31-54	XI-24-54	85	142	139	-3
<u>Lepomis microlophus</u>	Plastic	XI-24-54	XII-15-54	21	214	214	0

Table 2. Recaptures of tagged fish at Silver Springs, Florida.

Figure 1. Length-weight, Lepomis punctatus punctatus, Silver Springs, Florida, October 15, 1954.







## PRODUCTIVITY THEORY

H.T. Odum

## A. Optimum Efficiency--Maximum Power Principle Applied to Photosynthesis

In previous reports, the principle has been stated that open steady state systems tend to be adjusted at an optimum but low efficiency that corresponds to the maximum power output. (Odum and Pinkerton, American Scientist, in press) That this principle is valid for photosynthetic systems seems indicated in Figure 15 below:

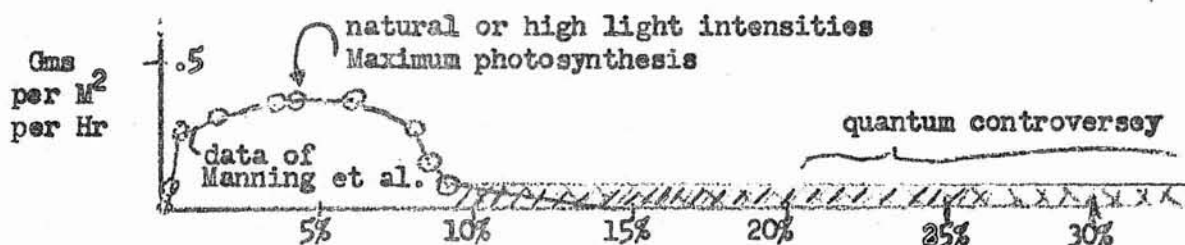


Figure 15. Photosynthesis versus efficiency indicating low but optimum efficiency associated with maximum output

This graph shows that high efficiencies such as have been achieved in all the work associated with the quantum controversy have all been at low light intensities so that the power output of glucose has been very small. On the other hand the natural populations of algae adjusted to high natural light intensities run at low efficiencies and high light intensities but so that a much greater output of glucose results. If plants are evolutionarily adapted to maximum output they must sacrifice efficiency for power by this hypothesis. This is a way of stating that attempts to increase world food by raising chlorella at high efficiencies must necessarily flop. A second part of this hypothesis may be stated that the optimum efficiency for maximum power output itself decreases as the light intensity increases. Plants adapted in nature to deep water achieve the optimum adjustment at a higher efficiency than at the surface. However, a plant adjusted for one light intensity can not be moved immediately to another light intensity and achieve the optimum adjustment without internal modification. A car climbing a hill in second gear at optimum efficiency cannot achieve the optimum efficiency for a straight away without changing gears. In the plant gears may be the concentration gradients. The efficiencies in Figure 15 are of the same magnitude at optimum adjustment as those found in Silver Springs and the Coral Reef.

## B. Organismal Size versus Metabolic Rate in Phototrophs in Optimum Adjustment

It is now well known that metabolism of heterotrophic organisms is inverse to body size roughly in a  $2/3$  power function that is presumed to be related to the surface/volume limits to diffusion processes. From the above section it was concluded that photosynthetic systems in open steady state tend to all become adjusted to a similar state of running at maximum power output because of the survival value in ecological competition both in an environmental and evolutionary sense. With similar light intensities, similar steady state plant systems should be adjusted to similar efficiencies and thus similar total photosynthetic power output of glucose on an AREA basis.

Now if the plants run at the same rate of output per area and if size effects hold for plants as well as animals, then small plants like *Chlorella* if growing in steady state should achieve the same output per area but with less biomass. The large climax rain-forest with big plants on the other hand if adjusted to the same light and optimum efficiency will require a much larger standing crop biomass because of the slower metabolism per pound of tissues.

In Figure 16 below is shown a graph of photosynthetic rate of plants of various minimum diameters under natural light or maximum photosynthetic adjustments. The data are from Verduin.

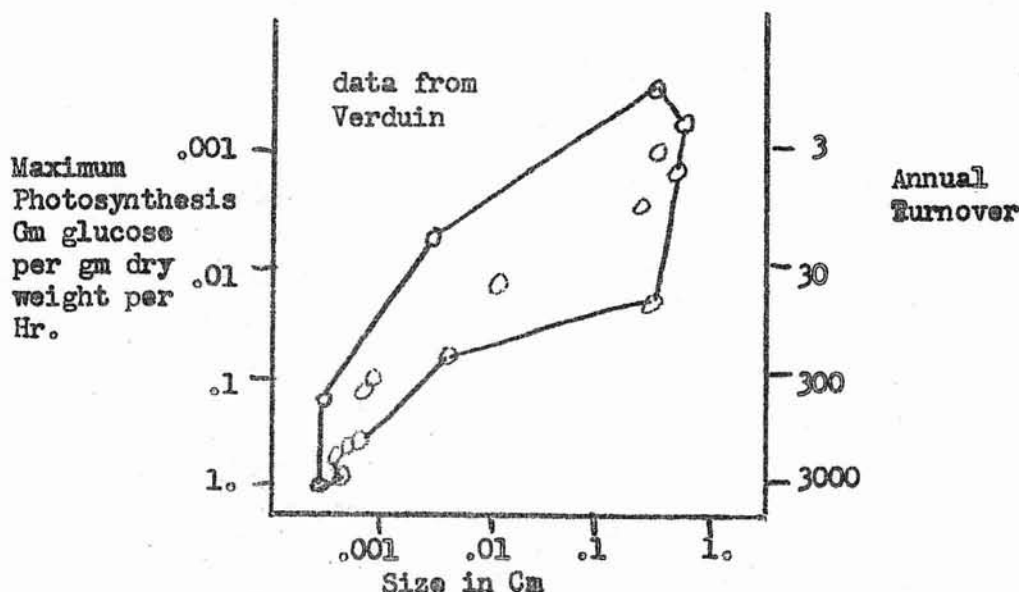


Figure 16. Effect of organismal size on Photosynthesis per weight

It is apparent that there is a size effect over a wide range just as in the heterotrophs. Thus, knowing the light intensity, the size of the producer, and the rough efficiencies found in given environments, one can compute the steady state biomass (carrying capacity).

### C. Pyramid Shape and Organismal Size

If as outlined above small sized producers put out the same production per area with a small biomass as do large producers with a large biomass both working at similar efficiencies, one can visualize two extreme types of pyramids as calculated in Figure 17. (For data showing similar efficiencies and production for mass *Chlorella* culture and grass plots see (Burlew: Mass Culture of Algae—Chapter 5—Wassink et. al., Carnegie, 1953)) In one the size of the organism decreases as one goes up the food chain as in grass—grasshopper—spider. In the other the size of the organism increases as one goes up the food chain as in *Chlorella*, paramecium, and fish. If the same energy passes up through both food chains with the same 10% efficiency for the higher trophic levels, two entirely different shaped pyramids of steady state biomass result because of the different rates of turnover. Some metabolic rate figures are used to compute Figure 17 from Heilbrunn's text. Photosynthetic values are taken from Figure 16.

The pyramids in Figure 17 help to visualize the possible relationship of the tropical ocean to the tropical rain forest. The small size of tropical plankters as well as the high temperature tend to cause the reversed pyramid calculated for *Chlorella*--*paramecium*--fish.

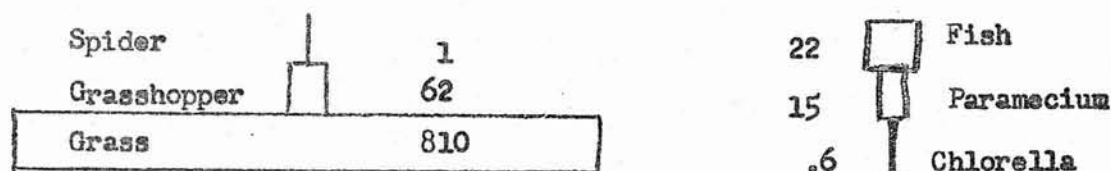


Figure 17. Two Extreme Pyramids with the Same Energy Flux showing the Dependence of biomass pyramid shape on organismal size.

#### D. Energy Contributions of Turbulence and Current, Plankton Size

The efficiencies of primary production so far estimated for Silver Springs (8%) and for the Eniwetok reef (6%) are considerably higher than many other natural communities or laboratory experiments run at high light intensities for maximum production. Since there is a large difference in nutrients between the reef and Silver Springs, it seems that some other property is in part responsible for this high production. It is reasonable to postulate that higher efficiencies are produced by the strong currents that serve as a community circulatory system, maintaining better nutrient concentrations adjacent to cells and removing waste products.

The effect of the circulation might be stated in two ways:

- A. The community receives energy from both the sun and from the current.
  - B. The energy directly from the sun goes further because of the current condition.
- If the usual efficiency at maximum adjustment is about 2%, about 5% might be postulated as due to the current system. This might imply that these flow systems derive more of their energy from primary production from the current energy than from the light received directly.

If current is as important as implied above, a suggestion can be made as to why larger and heavier phytoplankton usually prevail over smaller species with fat droplets so that they may float with the same density as water. Heavier plankters are maintained by the turbulent eddies so that they are continually falling through the currents that support them. This mechanism provides the cell with a local current which the organism at water density would not have. The relatively low *Chlorella* efficiencies obtained in high light intensity mass cultures in spite of high nutrients may be accounted for small size of *Chlorella* which decreases the effectiveness of stirring mechanisms.

#### E. Decrease of Daytime Plant Respiration Accounted for by the Hypothesis of Plant Respiratory Systems as herbivores of the Autotrophic systems--Arctic Significance

The data of several authors (i.e. Kok, see Rabinowitch) suggests that plant respiration in the daytime is much less than when the light is below the

compensation point. The concept of pyramids of biomass which may be supported during steady state suggests a reason. Whenever food energy is passed through an energy transformation step, a large percent, perhaps 90%, must go into heat as required by the second law of thermodynamics for these types of reactions under optimum efficiency—maximum power adjustments.

If a plant in the day can drive some of its work systems directly rather than making glucose first and then burning the glucose, the plant can save a step and thus avoid the heat loss from the extra step. Thus a higher efficiency in the heterotrophic system is maintained with less respiration. At night, by this view, it becomes necessary for the plant to fall back on glucose stored thus lengthening the chain of transformations and requiring increased respiration.

If true, this becomes especially significant when length of day and night is considered, for a little difference in day length means increased efficiency as well as additional light. There is less glucose that must be stored for use at the inefficient night rate. By this view Arctic plants during continuous daylight of summer should be much more efficient than similar temperate plants. On an annual basis however there would be no gain for the community would have to store many months worth of organic matter at the inefficient night rate.

#### F. Anaerobic Springs and the Saprobe System

The saprobe system of classifying pollution communities assumes the association of characteristic indicator species for different degrees of sewage type pollution. A consideration of Florida anaerobic springs shows that the system while useful when properly used has a fallacy that leads to misleading conclusions when used on waters in general.

Beecher, Orange, Warm Salt, and Volusia Co. Blue Spring are all examples of large springs with low organic content water that is also low in oxygen. The communities that result are both anaerobic and autotrophic in nature. In contrast sewage communities are anaerobic and heterotrophic. In the springs one gets sulfur bacteria and blue green algae but no ciliates. In short one gets some of the saprobe system biota in water that is the extreme opposite of sewage polluted water. Thoughtless use of the saprobe system leads to a complete misclassification of the type of primary production in these cases.

#### G. Some Definitions, Suggested methodology

In agriculture, man's continued labor and supervision guise a complex community in a direction he desires. However in Ecological Engineering the outcome of production of a complex community is achieved by proper selection of components at the start with subsequent hands off thus permitting the community to reach a unique steady state adjustment.

In the usual scientific experiment, man controls one variable so as to study the behavior of another dependant variable while holding other conditions constant. Thus the process is one of analyzing component processes. In Microcosm experimentation on the other hand components are put together and the complex allowed to make its own trends under observation.

The study of ecological engineering by microcosm experimentation is a practical methodology for studying the synthesis of ecological systems. This springs project is an example of the microcosm approach.



A hypothesis regarding dependence of community  
structure and density on productivity

by J. L. Yount

The hypothesis is offered that under similar general conditions the species variety is an inverse function of the community productivity.

The salps of a series of plankton samples made by Pacific Oceanic Fishery Investigations of the United States Fish and Wildlife Service in epipelagic waters of the central Pacific Ocean were studied during 1952-1954. Observations on them led to the formulation of the hypothesis presented below. The most pertinent observations were as follows. In most of the samples studied, many species of salps were taken with little predominance of any one species. In one sample, however, there were both a far greater total salp quantity and a great predominance of one species of salp, only a few others being taken and these in insignificant quantities. All salp species apparently simultaneously occupy similar niches (the concept of the niche used here is that of Elton, 1927, Animal Ecology: 63-4), and apparently also are subject to the same environmental conditions, thus apparently are ecological equivalents (in impoverished waters; see below).

Observations made by other investigators are also pertinent here. Students of marine plankton of high latitudes have described it as "monotonous", consisting predominantly of one species of organism in each niche apparently, although the term niche has not been applied in these descriptions. Most descriptions of the plankton of low latitudes, however, emphasize the great variety of species with little or no predominance by any one species (per niche) (see Steuer, 1910, Planktonkunde: 601-4; Russell and Yonge, 1936, The Seas: 123-6; Dakin and Colefax, 1940, The Plankton of the Australian Coastal Waters off New South Wales, Univ. Sydney, Dept. Zoology, Publ. I: 27-34). Another pertinent observation discussed by Steuer and Dakin is that productivity in the tropics in waters influenced by land drainage and in regions of upwelling may equal or even exceed that of high latitudes.

If these observations are considered together, it appears that in epipelagic waters with relatively great quantities of nutrient chemicals (the enriched areas), production of the plankton is great in quantity but trends toward few species of organisms--probably only one dominant species per niche--and in epipelagic waters with relatively small quantities of nutrient chemicals (the impoverished areas), the plankton is small in quantity and trends toward many species of organisms--apparently many species per niche.

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If the plankton now be compared to sessile organisms of the Aufwuchs and benthos, it will be seen that the two groups have similar natures, in that sessile organisms and plankters are moderately passive in ability to capture food and to move in their medium (most sessile organisms, of course, move during some phase of their life cycle, and plankters have some ability to move, but directed movement is limited for both). For this reason, at least the plankton and sessile organisms probably should be considered together in the hypothesis.

It is postulated from these observations that if productivity is low and other factors are constant, species of ecologically passive organisms at least, may occur together as ecological equivalents with little or no predominance of one species in each niche; and conversely if productivity is high and other factors are constant, species of these organisms should not occur together as ecological equivalents, but rather one species should dominate in each niche. This leads to a further postulate: if productivity is low and other factors are constant, competition and other coactions should be reduced for these organisms; whereas if productivity is high and other factors are constant, competition and other coactions should be increased for them.

The following evidences tend to support this hypothesis. In the tropic epipelagic holoplankton, productivity is low and quantity is small, except in certain regions mentioned above, and species numbers are great; in the epipelagic holoplankton of high latitudes, productivity is high and quantity is great, but species numbers are small. Occasionally in tropic waters, swarms of plankters appear, consisting of few species of organisms and a relatively great quantity--productivity is therefore high and species numbers few, even in the midst of impoverished waters, under enriched conditions. In plankton tows from impoverished waters, many species of organisms occur together that apparently are ecological equivalents, and this is evidently not true of plankton tows from enriched waters (evidences for this statement are based chiefly on studies of salps, but it is postulated as being true of other plankters as well). In Florida Springs, it has been noted (H. T. Odum, L. A. Whitford, W. C. Sloan) that productivity is high and the number of species of the various groups of organisms is low.

This hypothesis is being tested at present with Aufwuchs growth under the controlled conditions of the Florida Springs and, if results warrant, is expected to be tested under other fresh water and marine conditions. Counts of Aufwuchs species numbers on slides, relative to current controlled total productivity, have been started. Counts made on the preliminary first series are consistent with the hypothesis.